Herbivore harvesting and alternative steady states in coral reefs

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BIOMAT 2017 *INM, RAS, MOSCOW*

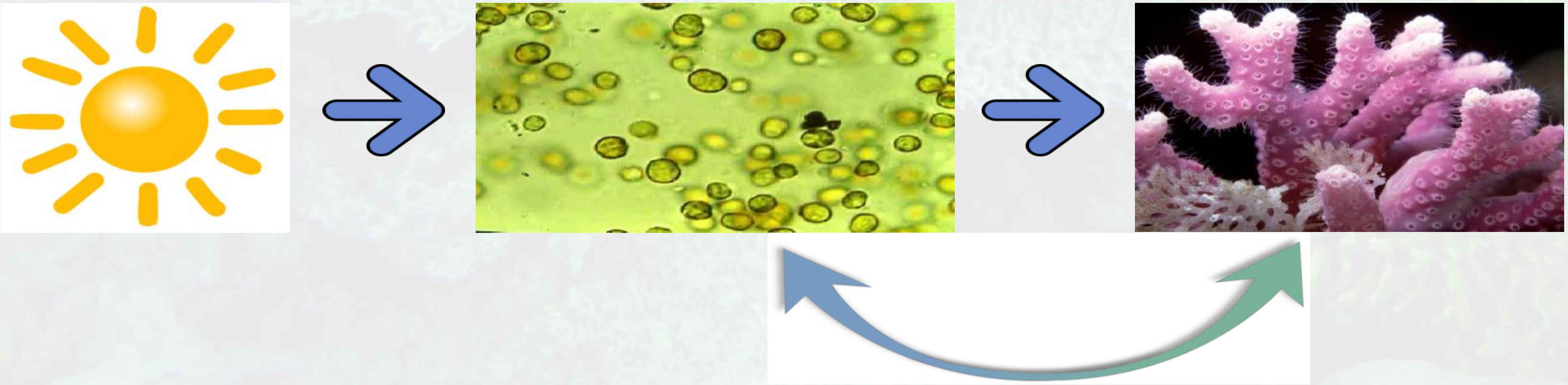
Outline

- Introduction
- Phase Shifts in coral-reefs
- Model Construction
- Stability Property of different Equilria of model
- Bifurcation analysis
- System with delay
- Effect of macroalgal toxicity and overfishing on the resilience of coral reefs
- Observations

Biological Overview (contd.)

- The Coral Reef Ecosystem is a diverse collection of species that interact with each other and the physical environment. It is the essential feeding and breeding ground for numerous organisms.

- The Sun is the initial source of energy for this ecosystem.



Biological Overview

- **Turf algae** are multispecific assemblage of microalgae that attain a canopy height of only 1-10 mm.

- **Macroalgae** are larger (canopy height usually >10mm) erect algae often with anatomically complex forms.

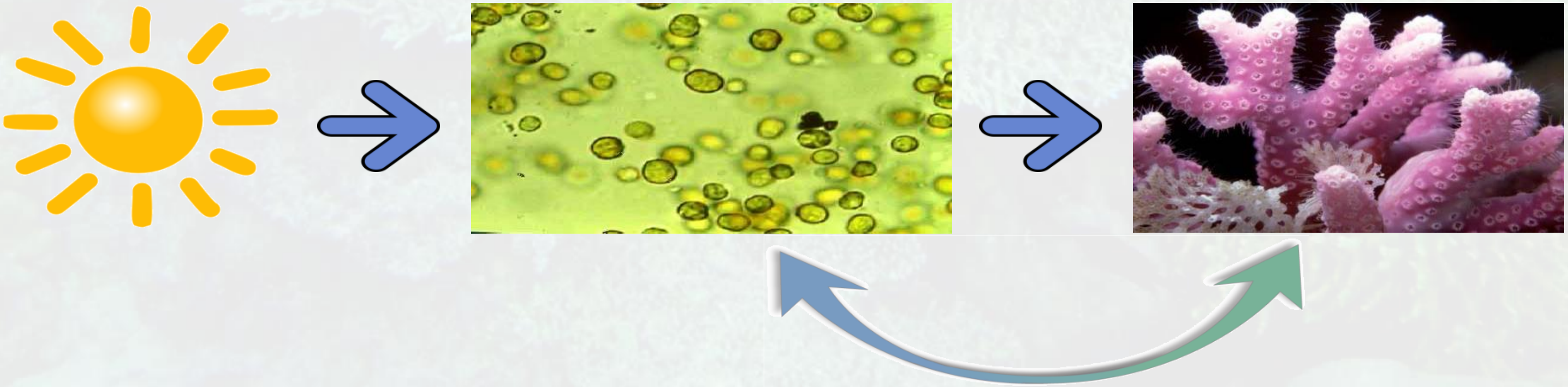
- Corals settle on turf algae. Macroalgae spread vegetatively over turf algae.

- High macroalgal biomass can interfere with coral recruitment and reduce coral survival.

Symbiotic relation between Zooxanthella and Coral polyps

- Coral polyps do not photosynthesize, but have a symbiotic relationship with single-celled organisms called Zooxanthellae living inside coral polyp tissues.

- Through photosynthesis, Zooxanthellae produces O_2 and carbohydrates for coral polyps. In return, coral polyps produces CO_2 and ammonia for Zooxanthella.



Cause of Concern

Coral Bleaching: It is the result of disruption of symbiosis between Zooxanthella and coral hosts.

Coral Bleaching due to macroalgal toxicity

- Toxin released by macrocalgae increases the mortality rate of corals. During HAB, large areas of corals becomes depleted.

Coral Bleaching due to overfishing

- In absence of herbivorous Parrotfish, there is a rapid increase of growth of sea weeds.
- Coral polyps are smothered to death by this rapid growth of algal mats, resulting to coral bleaching.

Bhattacharyya and Pal: *Nonlinear Analysis: Real World Applications*,**12**, 965-978, (2011)

Phase shifts in coral-reefs

- Coral reefs can undergo relatively rapid changes in the dominant biota, a phenomenon referred to as **phase shift**.
- Degradation of coral reefs is often associated with changes in community structure towards macro-algal dominated reef ecosystem due to the reduction in herbivore caused by overfishing.
- We investigate coral-macroalgal phase shift due to the effects of harvesting of herbivorous reef-fish by means of a continuous time model in a food chain.

Bhattacharyya and Pal: JBP,39, 37-65 **(2013)**

Bhattacharyya and Pal: CMWA, 66(3), 339–355, 2013.

Hysteresis in Ecology

- In ecology, ecosystems can exist under multiple alternative steady states. Under external perturbations, these ecosystems may exhibit **phase shifts**.
- Due to ecological feedbacks, ecosystems display resistance to phase shifts and therefore tend to remain in one state unless perturbations are large enough. Multiple states may persist under equal environmental conditions, a phenomenon known as **hysteresis**.

Bhattacharyya and Pal, JBP (2015)

Bhattacharyya and Pal, Ecological Complexity (2015)

Bhattacharyya and Pal, Ecological Complexity (2015)

Basic Assumptions

- $M(t)$, $C(t)$ and $T(t)$ represent the fractions of the seabed area covered by [illegible] algal turf and [illegible] respectively at time t.
- The grazing rate of herbivores on macroalgae is [illegible], where β represents the harvest-mediated reduction in grazing.
- Grazing of macroalgae by herbivores give rise to [illegible]
- Toxin induced death rate of corals is [illegible]
- Grazing on algal turfs prevents the vegetative [illegible]

Basic Assumptions (contd.)

- Macroalgae spread vegetatively over algal turfs at a rate a.
- Colonization rate of newly immigrated macroalgae on algal turf is b.
- Corals recruit to and overgrow algal turfs at a rate r.
- Corals are overgrown by macroalgae at a rate α.
- Death of macroalgae and corals is adding to the growth of turf algae.
- The loss of macroalgal cover and subsequent recolonization of algal turfs due to grazing.

$$\frac{dM}{dt} = aMT + bT + \alpha MC - d_1 M - \frac{g(1-\beta)M}{C+T}$$

$$\frac{dT}{dt} = -aMT - bT - rTC + (d_1 M + d_2 C) + \frac{g(1-\beta)M}{C+T} + \gamma MC$$

$$\frac{dC}{dt} = rTC - \alpha MC - d_2 C - \gamma MC$$

Effect of Macroalgal toxicity

Simplification of the model

Since $\frac{d}{dt}(M + C + T) = 0$, it follows that $M(t) + C(t) + T(t) = c_0$, for all $t \geq 0$, where $c_0 = M(0) + C(0) + T(0)$.

Without any loss of generality we assume that $c_0 = 1$. Then the system reduces to

$$\begin{aligned} \frac{dM}{dt} &= M\left\{\alpha C - \frac{g(1-\beta)}{1-C} - d_1\right\} + (aM + b)(1 - M - C) \equiv f^1 \\ \frac{dC}{dt} &= C\left\{r(1 - M - C) - (\alpha + \gamma)M - d_2\right\} \equiv f^2 \end{aligned} \qquad (2)$$

where $M(0) \geq 0$ and $C(0) \geq 0$.

Equilibria

The system (2) possesses the following equilibria:

(i) Coral-free equilibrium $\boxed{E_0 = (M_0, 0)}$, where $M_0 = \frac{a-b-d_1-g(1-\beta)+\sqrt{\{a-b-d_1-g(1-\beta)\}^2+4ab}}{2a}$;

(ii) interior equilibrium $\boxed{E^* = (M^*, C^*)}$, given by the intersections of the nullclines

$M\left\{\alpha C - \frac{g(1-\beta)}{1-C} - d_1\right\} + (aM+b)(1-M-C) = 0$ and $r(1-M-C) = (\alpha+\gamma)M + d_2 = 0$

in the interior of the first quadrant. C^* is given by the equation $a_1C^3 + a_2C^2 + a_3C + a_4 = 0$

and $M^* = p + qC^*$, where

$a_1 = q\{a(1+q) - \alpha\}, a_2 = q(\alpha + d_1) - \alpha p - aq(1-p) + (1+q)(b + ap - aq)$,

$a_3 = p(\alpha + d_1) - q\{d_1 + g(1-\beta)\} + (1-p)(aq - ap - b) - (1+q)(ap + b)$,

$a_4 = (ap+b)(1-p) - p\{d_1 + g(1-\beta)\}, p = \frac{r-d_2}{r+\alpha+\gamma}$ and $q = \frac{-r}{r+\alpha+\gamma}$.

Stability Analysis

At E_0 the eigenvalues of the Jacobian matrix of the system (2) are $-\sqrt{\{a-b-d_1-g(1-\beta)\}^2+4ab}$ and $r-M_0(r+\alpha+\gamma)-d_2$. Therefore, all the eigenvalues of the Jacobian matrix are negative if $r-M_0(r+\alpha+\gamma)-d_2<0$. This gives the following lemma:

Lemma 3.1. *The system (2) is locally asymptotically stable at E_0 if $\gamma>\gamma_*$, where $\gamma_*=\frac{r-d_2-M_0(r+\alpha)}{M_0}$.*

Therefore, with high macroalgal toxicity, corals are eliminated from the system.

Lemma 3.2. *If $r>\frac{f^1_{M|E^*}}{C^*}$ and $(r+\alpha+\gamma)f^1_{C|E^*}>rf^1_{M|E^*}$, the system (2) is locally asymptotically stable at E^*.*

Therefore, with high coral-encroachment on algal turfs, the interior equilibrium becomes locally asymptotically stable.

Non-existence of periodic solutions

We consider the Dulac function (Hsu & Huang, 1995) $B(M, C) = \frac{1}{MC}$, where $M, C > 0$.

Then at (M^*, C^*), we have $\nabla.(Bf^1, Bf^2) = -\frac{1}{C^*}\left\{a + \frac{rC^*}{M^*} + \frac{b(1-C^*)}{M^{*2}}\right\} < 0$.

Since this divergence has constant sign throughout the first quadrant, by Dulac's criterion (Strogatz, 1994) we get the following lemma:

Lemma 3.3. *The system* (2) *has no closed orbit contained in the first quadrant.*

Since there is no periodic solution for the system (2) in the first quadrant, by Poincare-Bendixon theorem, it follows that every trajectory of the system (2) approaches asymptotically to an equilibrium point of the system (2).

Transcritical bifurcation at E_0

Lemma 3.4. *The system* (2) *undergoes a transcritical bifurcation at* E_0 *when* γ *crosses* γ_*.

Proof: At $\gamma = \gamma_*$, we have

$$J_0 = \begin{pmatrix} -\sqrt{\{a-b-d_1-g(1-\beta)\}^2+4ab} & M_0\{\alpha-a-g(1-\beta)\}-b \\ 0 & 0 \end{pmatrix}$$

Therefore, the zero eigenvalue of the Jacobian matrix is simple.

Let V and W be the eigenvectors corresponding to the zero eigenvalue for J_0 and J_0^T respectively.

Then we obtain $V = \begin{pmatrix} 1 & v_1 \end{pmatrix}^T$ and $W = \begin{pmatrix} 0 & 1 \end{pmatrix}^T$, where $v_1 = \frac{\sqrt{\{a-b-d_1-g(1-\beta)\}^2+4ab}}{M_0\{\alpha-a-g(1-\beta)\}-b}$.

Transcritical bifurcation at E_0 contd.

Let us express the system (2) in the form $\dot{X} = f(M, C)$, where

$$X = \begin{pmatrix} M & C \end{pmatrix}^T \text{ and } f(M, C; \gamma) = \begin{pmatrix} f^1 & f^2 \end{pmatrix}^T$$

Then $W^T f_\gamma(M_0, 0; \gamma_*) = 0$.

Thus, no saddle-node bifurcation occurs at E_0 when γ crosses γ_*.

Also, $D^2 f(M_0, 0; \gamma_*)(V, V) = \left[\frac{\partial^2 f(M,C;\gamma_*)}{\partial M^2} + \left(\frac{\partial^2 f(M,C;\gamma_*)}{\partial M \partial C} + \frac{\partial^2 f(M,C;\gamma_*)}{\partial C \partial M}\right) v_1 + \frac{\partial^2 f(M,C;\gamma_*)}{\partial C^2} v_1 v_1\right]_{(M,C)=(M_0,0)}$

$= -2v_1(r + \alpha + \gamma_* + r v_1) \neq 0.$

Therefore, the system (2) undergoes a transcritical bifurcation at E_0 when γ crosses γ_*.

Saddle-node bifurcation at E^*

Lemma 3.5. *If* $r > \frac{f^1_{M|E^*}}{C^*}$ *and* $\gamma^* \neq \eta$*, the system* (2) *undergoes a saddle-node bifurcation at* E^* *when* γ *crosses* γ^**, where* $\gamma^* = \frac{r f^1_{M|E^*}}{f^1_{C|E^*}} - r - \alpha$ *and* $\eta = \frac{2ar^3(1-C^*)^3}{g(1-\beta)\{r(1-C^*)+d_2\} - 2r^2(\alpha-a)(1-C^*)^3} - r - \alpha$.

Proof: If $r > \frac{f^1_{M|E^*}}{C^*}$ and $\gamma = \gamma^*$, then $Tr(E^*) \neq 0$ and $Det(J^*) = 0$ and so, the zero eigenvalue of the Jacobian matrix is simple.

At $\gamma = \gamma^*$ we have $J^* = \begin{pmatrix} f^1_{M|E^*} & f^1_{C|E^*} \\ -\frac{rC^* f^1_{M|E^*}}{f^1_{C|E^*}} & -rC^* \end{pmatrix}$

Let V^* and W^* be the eigenvectors corresponding to the zero eigenvalue for J^* and J^{*T} respectively.

Then we obtain $V^* = \begin{pmatrix} 1 & -\frac{r+\alpha+\gamma^*}{r} \end{pmatrix}^T$ and $W^* = \begin{pmatrix} 1 & \frac{f^1_{C|E^*}}{rC^*} \end{pmatrix}^T$.

Saddle-node bifurcation at E^* contd.

We obtain, $W^T f_\gamma(M^*, C^*; \gamma^*) = -\frac{M^* f^1_{C|E^*}}{r} \neq 0$.

Also, $D^2 f(M^*, C^*; \gamma^*)(V, V) = -2a - \frac{2(r+\alpha+\gamma^*)(\alpha-a)}{r} + \frac{g(1-\beta)(r+\alpha+\gamma^*)\{r(1-C^*)+d_2\}}{r^3(1-C^*)^3} \neq 0$ if $\gamma^* \neq \eta$, where $\eta = \frac{2ar^3(1-C^*)^3}{g(1-\beta)\{r(1-C^*)+d_2\}-2r^2(\alpha-a)(1-C^*)^3} - r - \alpha$.

Therefore, if $r > \frac{f^1_{M|E^*}}{C^*}$ and $\gamma^* \neq \eta$, the system (2) undergoes a saddle-node bifurcation at E^* when γ crosses γ^*.

Hysteresis

Assume that the conditions of Lemma 3.4 and 3.5 are satisfied. If $\gamma_* < \gamma^*$ holds, a sharp transition with hysteresis occurs.

Numerical Simulations

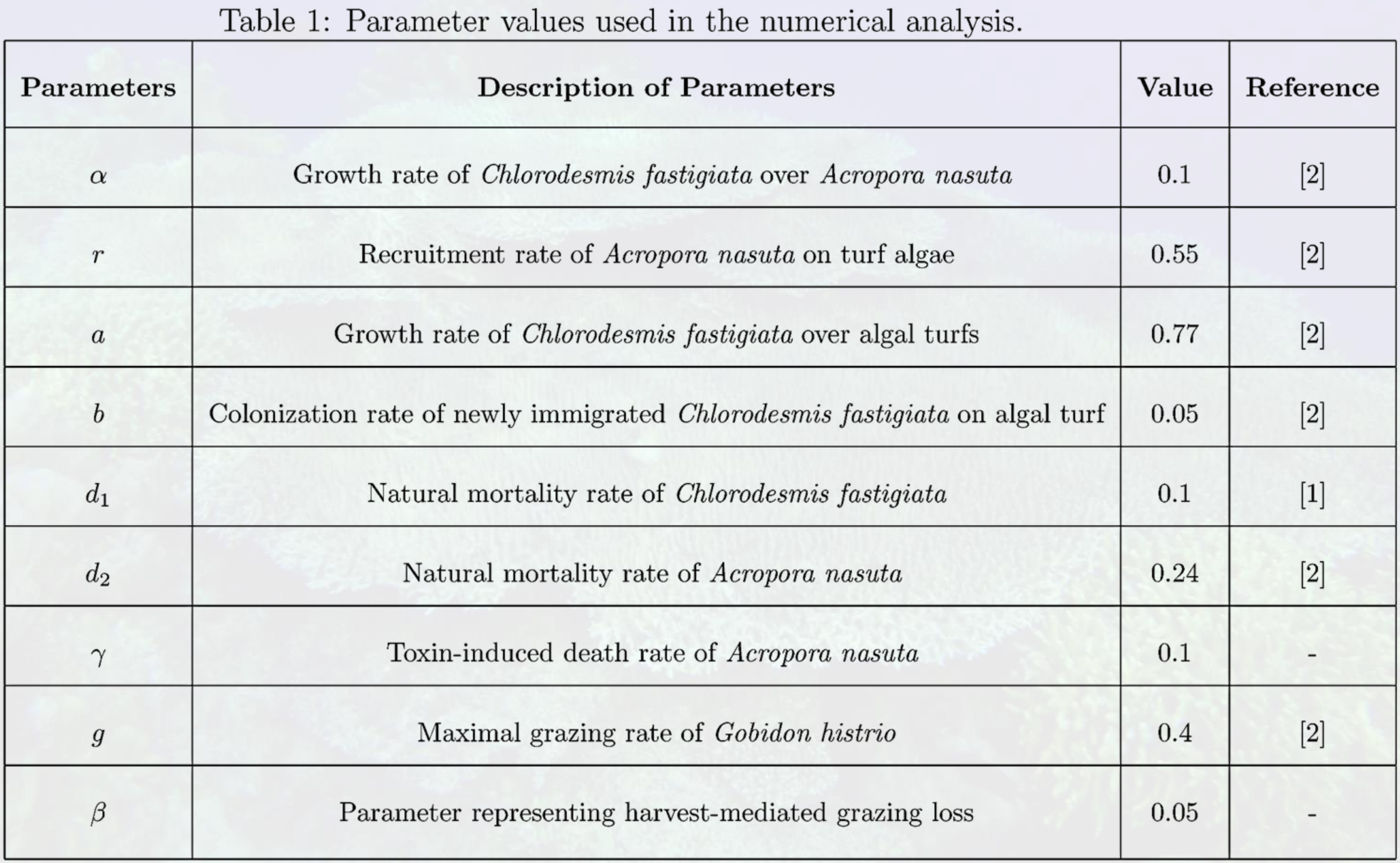
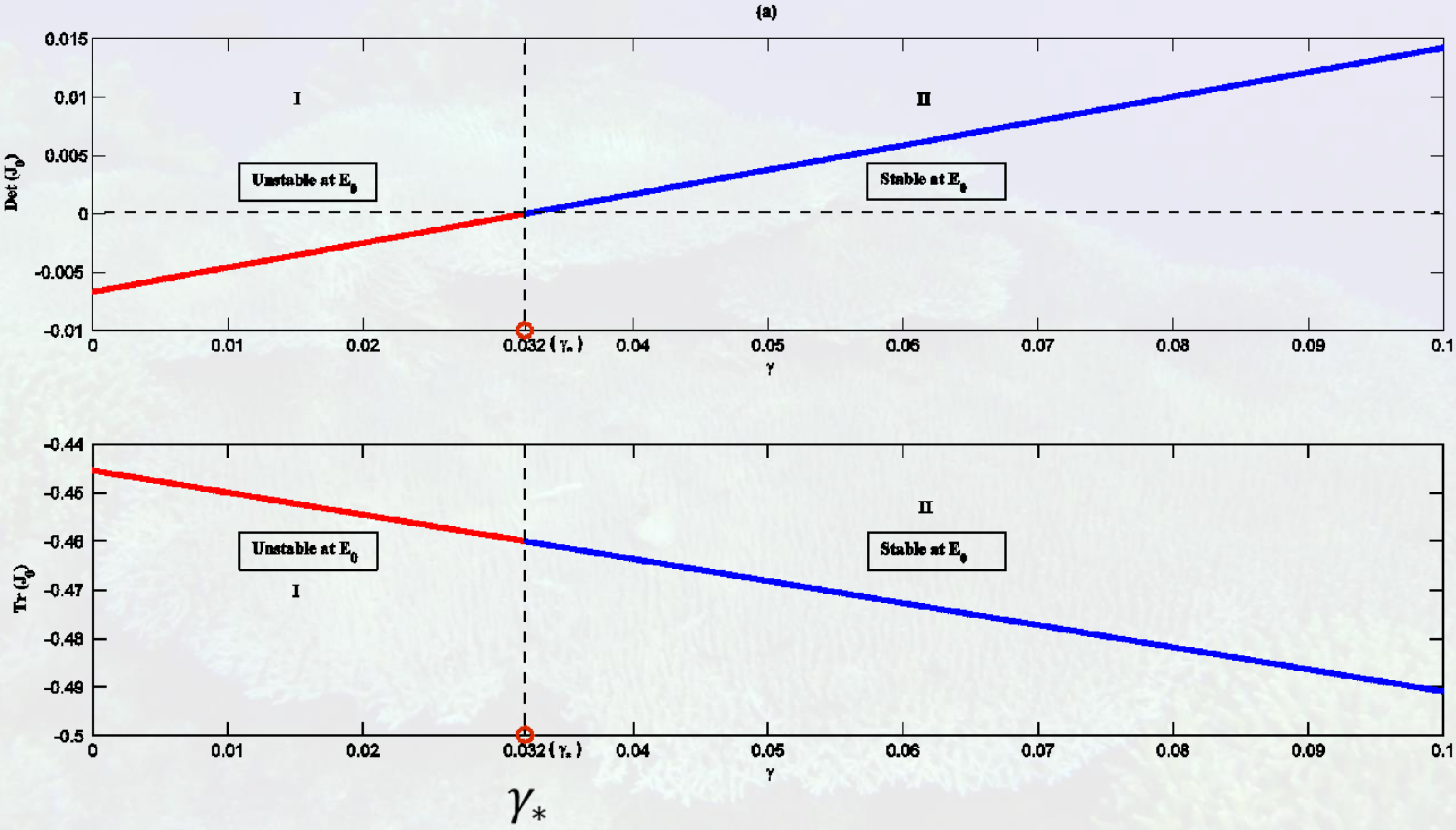


Table 1: Parameter values used in the numerical analysis.

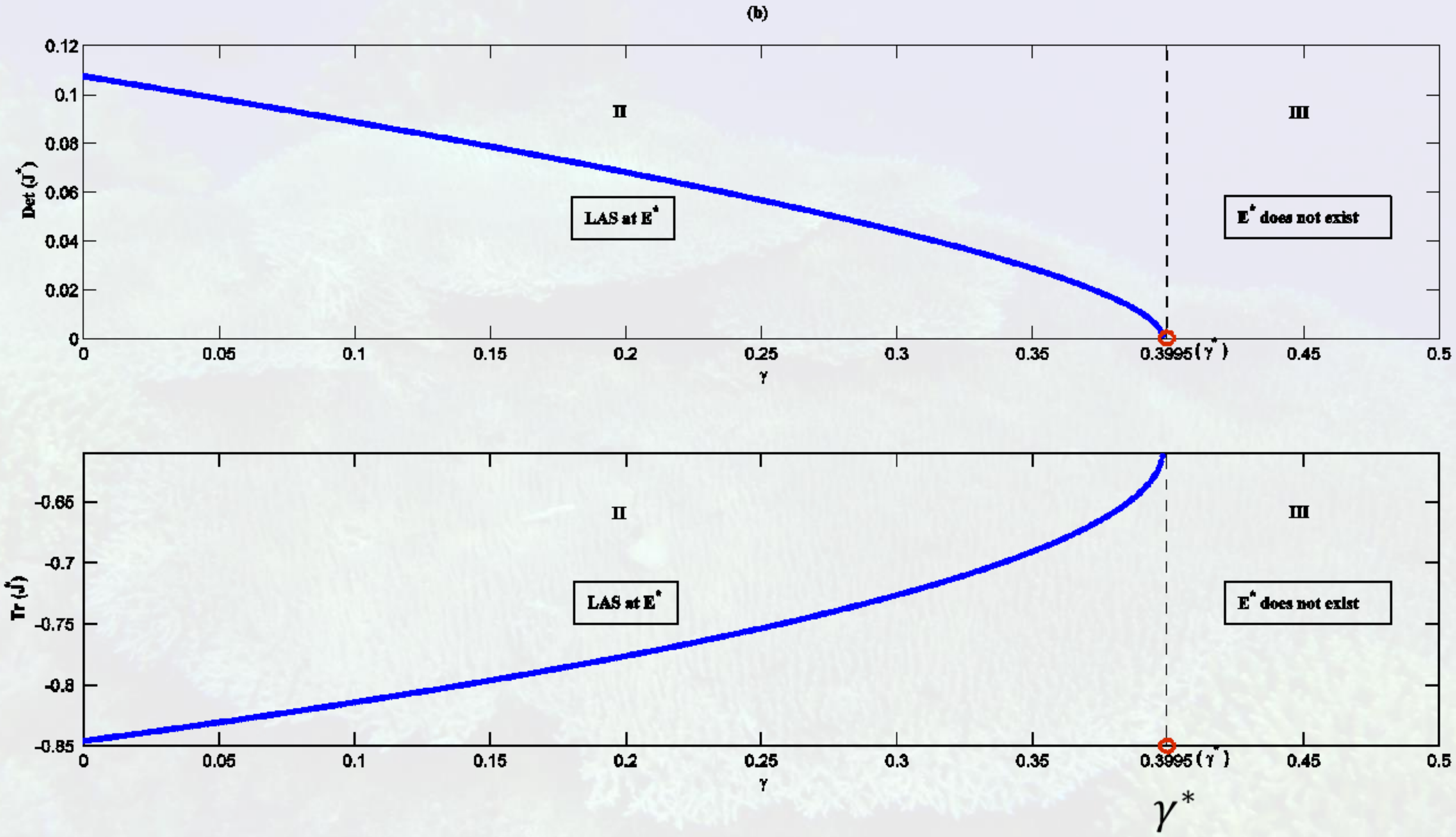
Parameters	**Description of Parameters**	**Value**	**Reference**
α	Growth rate of *Chlorodesmis fastigiata* over *Acropora nasuta*	0.1	[2]
r	Recruitment rate of *Acropora nasuta* on turf algae	0.55	[2]
a	Growth rate of *Chlorodesmis fastigiata* over algal turfs	0.77	[2]
b	Colonization rate of newly immigrated *Chlorodesmis fastigiata* on algal turf	0.05	[2]
d_1	Natural mortality rate of *Chlorodesmis fastigiata*	0.1	[1]
d_2	Natural mortality rate of *Acropora nasuta*	0.24	[2]
γ	Toxin-induced death rate of *Acropora nasuta*	0.1	-
g	Maximal grazing rate of *Gobidon histrio*	0.4	[2]
β	Parameter representing harvest-mediated grazing loss	0.05	-

Transcritical bifurcation at γ_*



$(a)\ At\ \gamma_*, Det(J_0) = 0\ and\ Tr(J_0) < 0\ with\ instability\ at\ E_0\ for\ \gamma < \gamma_*\ and\ stability\ at\ E_0\ when\ \gamma > \gamma_*.$

Saddle-node bifurcation at γ^*



$(b) At\ \gamma^*, Det(J^*) = 0\ and\ Tr(J^*) < 0\ with\ stability\ at\ E^*\ for\ \gamma < \gamma^*\ and\ non - existence\ of\ E^*\ when\ \gamma > \gamma^*.$

Bifurcation diagram of γ vs. the equilibrium value of coral cover.

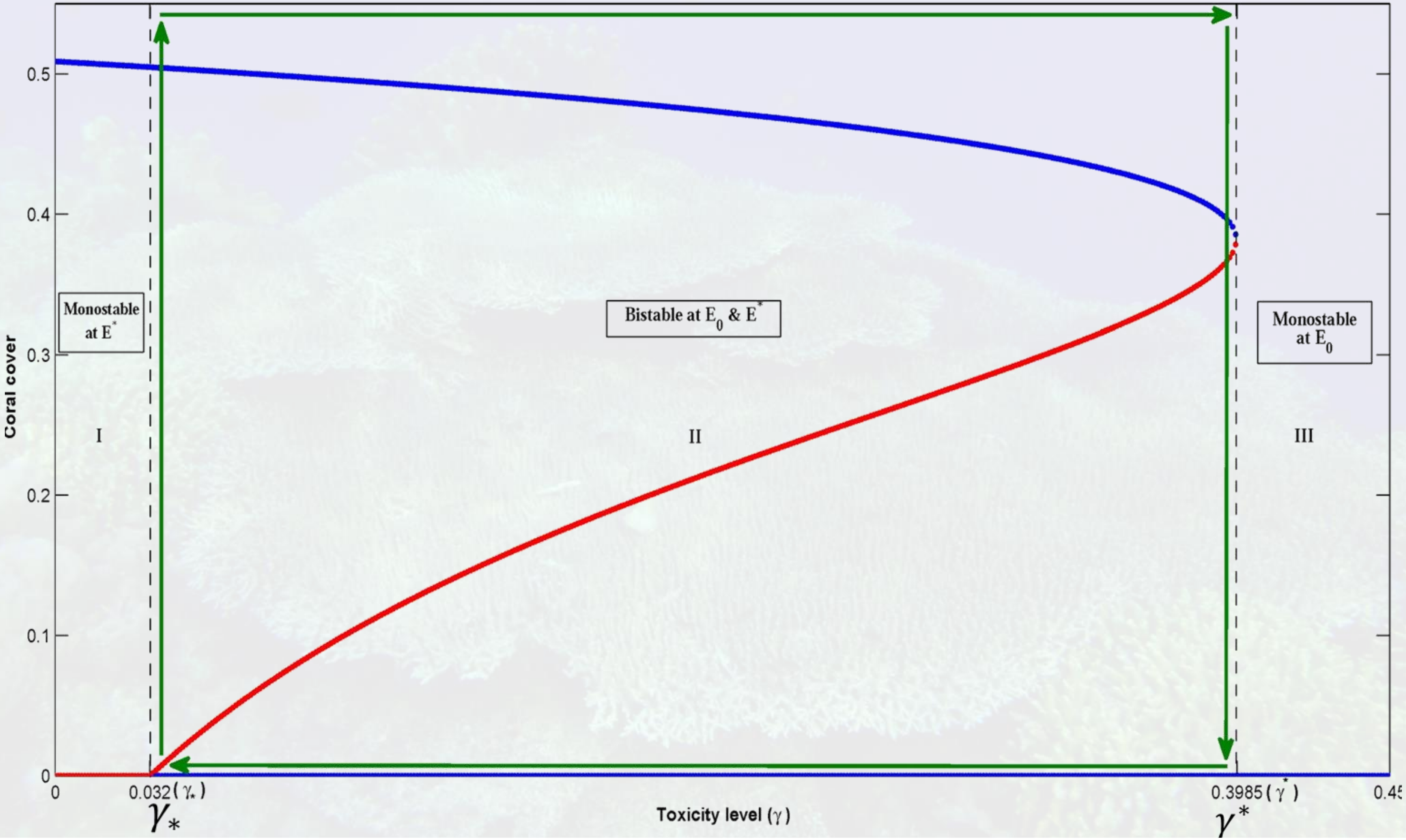
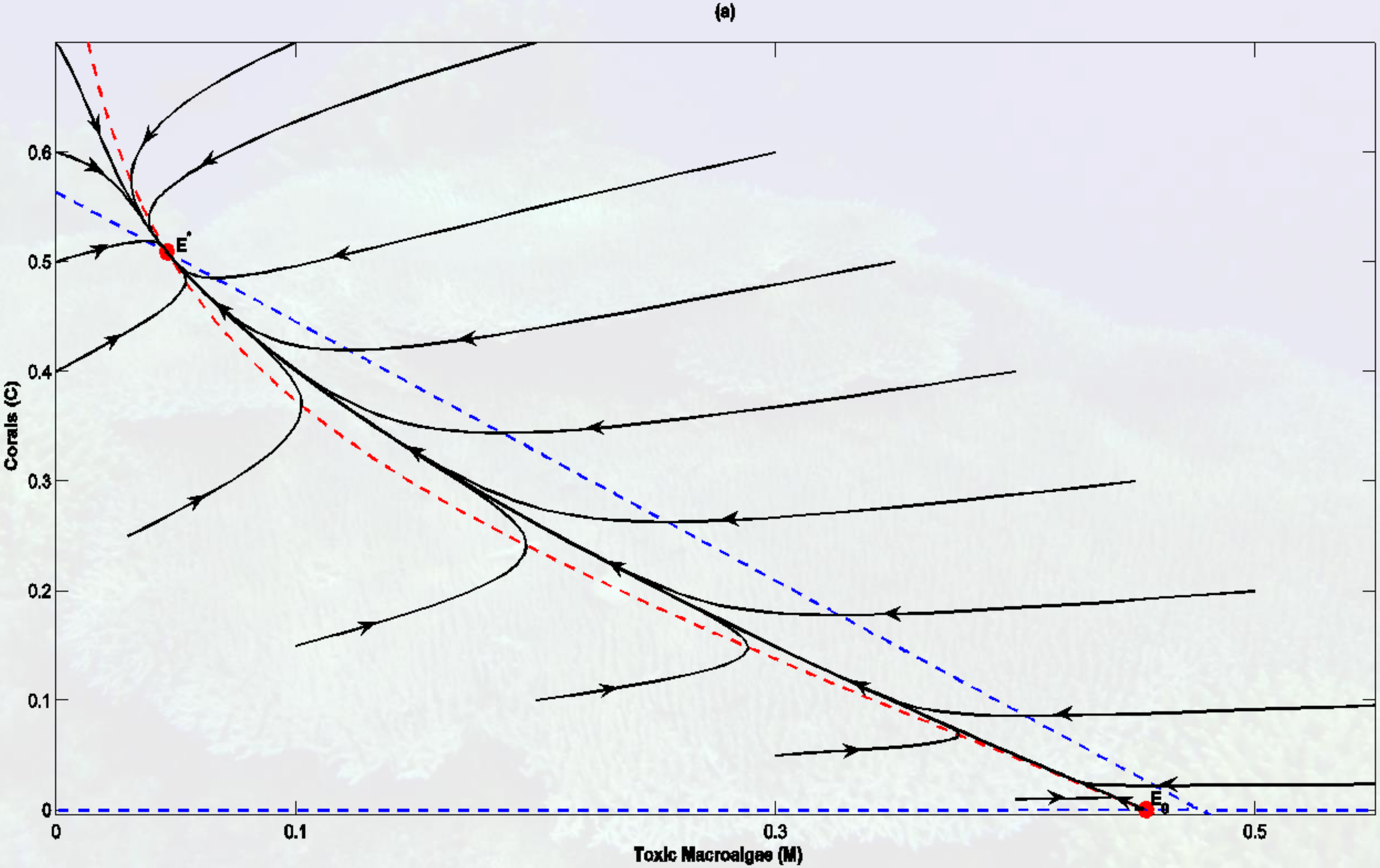


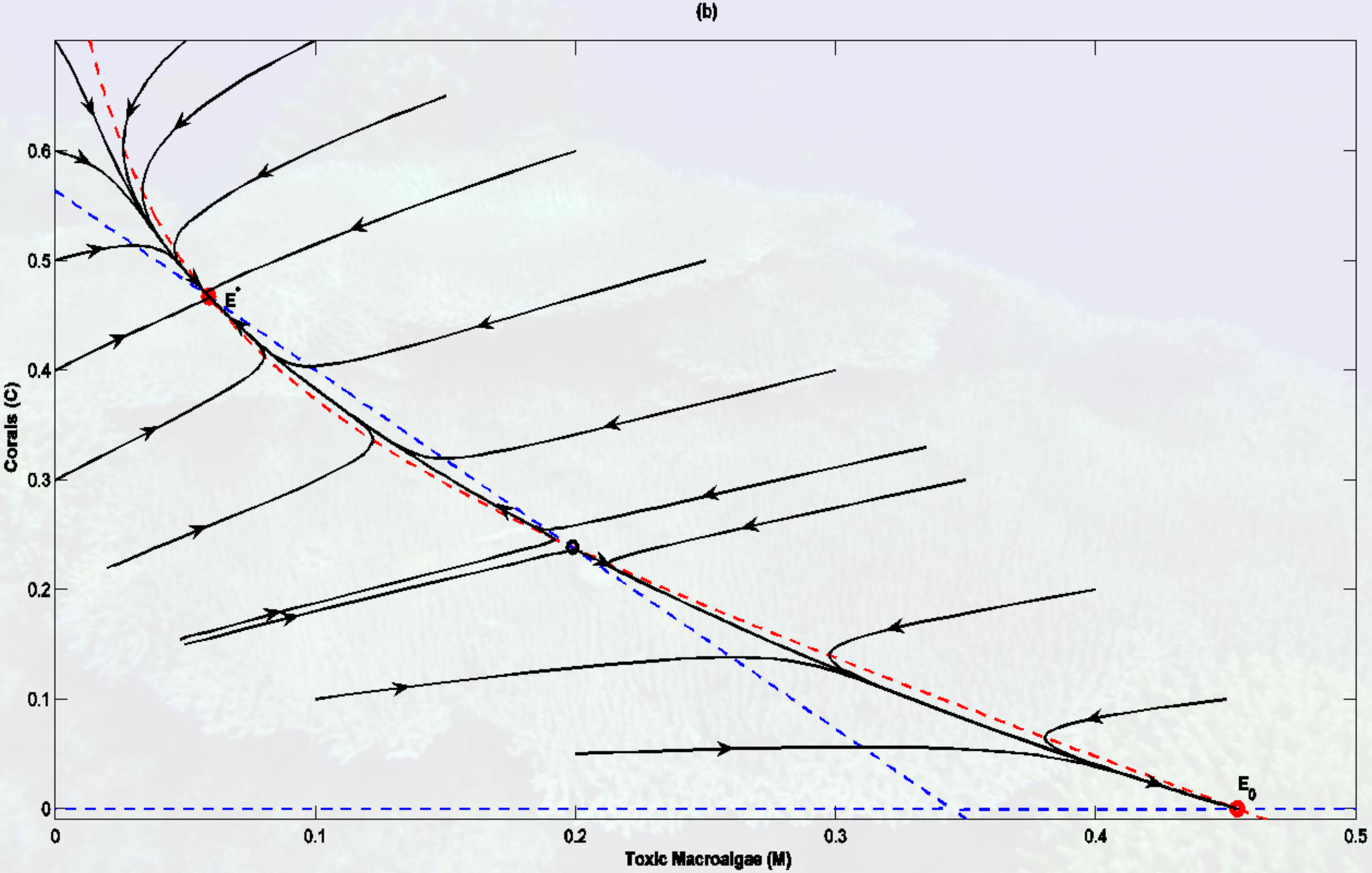
Figure 1: Bifurcation diagram of macroalgal toxicity (γ) versus the equilibrium value of coral cover, demonstrating the possibility of hysteresis ($\gamma_* < \gamma^*$) with the hysteresis loop depicted by arrows. Stable equilibria are indicated by blue lines, unstable equilibria by red lines.

Monostable at E*



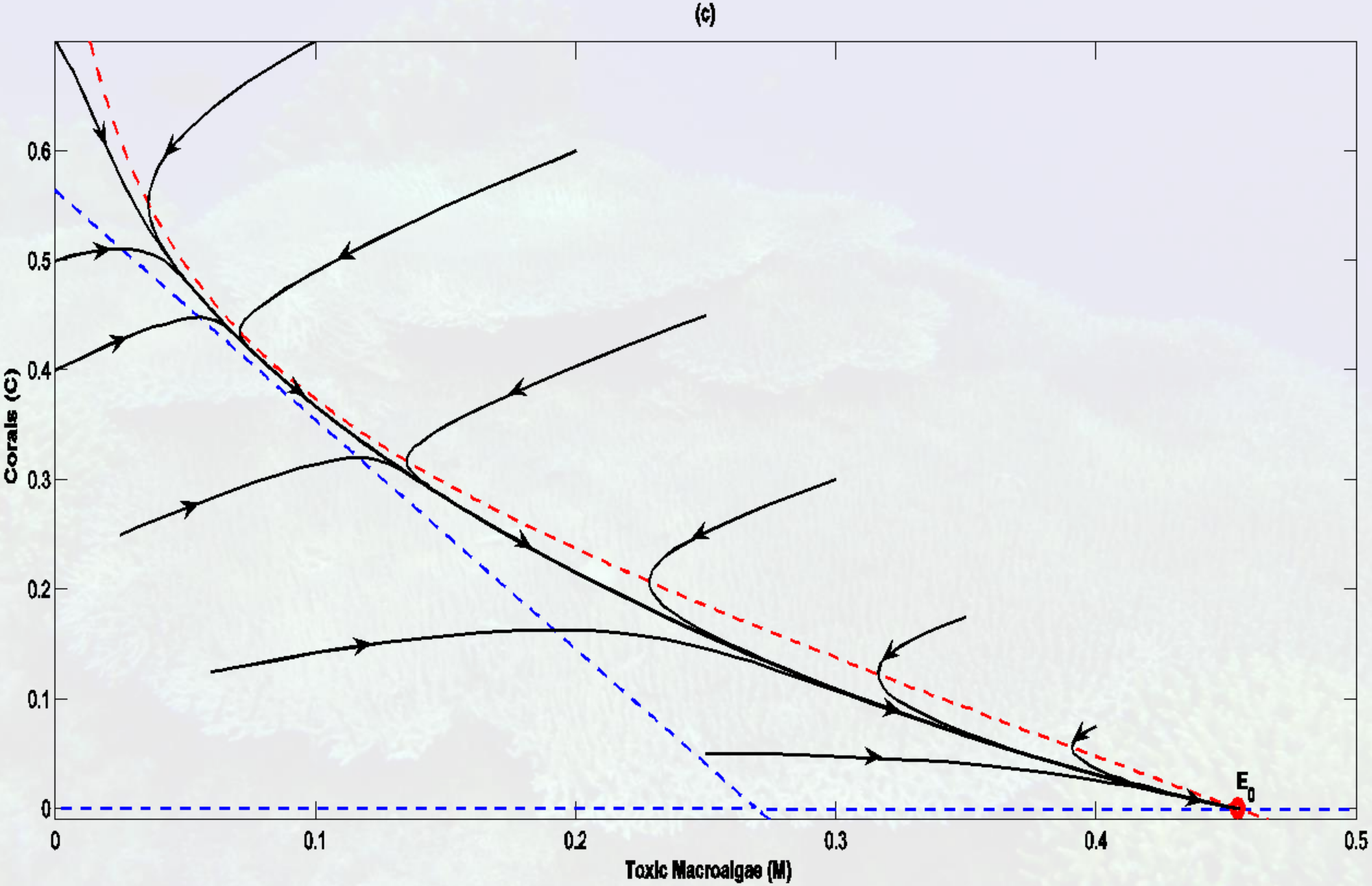
Region I ($\gamma = 0$)

Bistable at E_0 and E^*



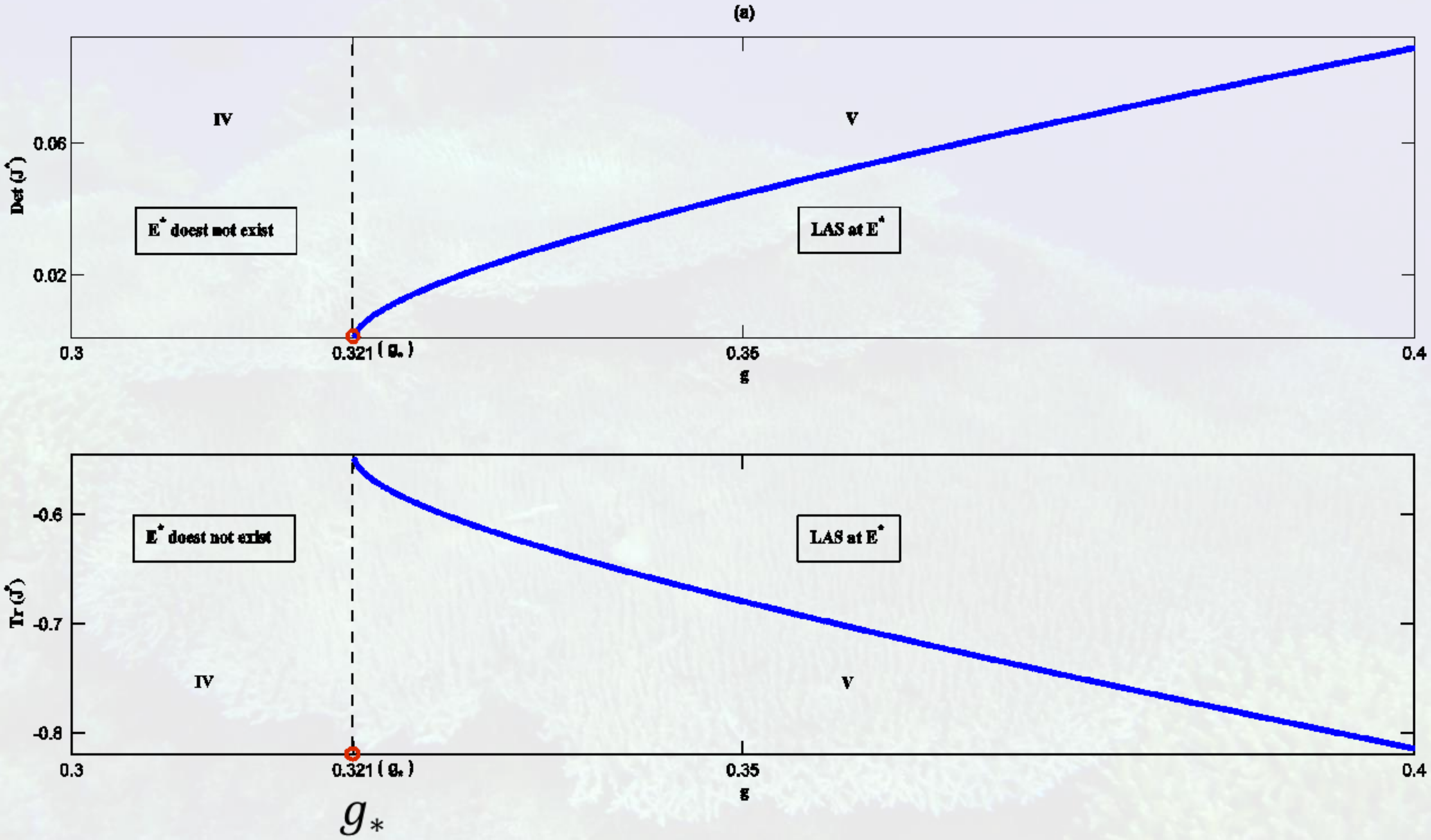
Region II ($\gamma = 0.25$)

Monostable at E_0



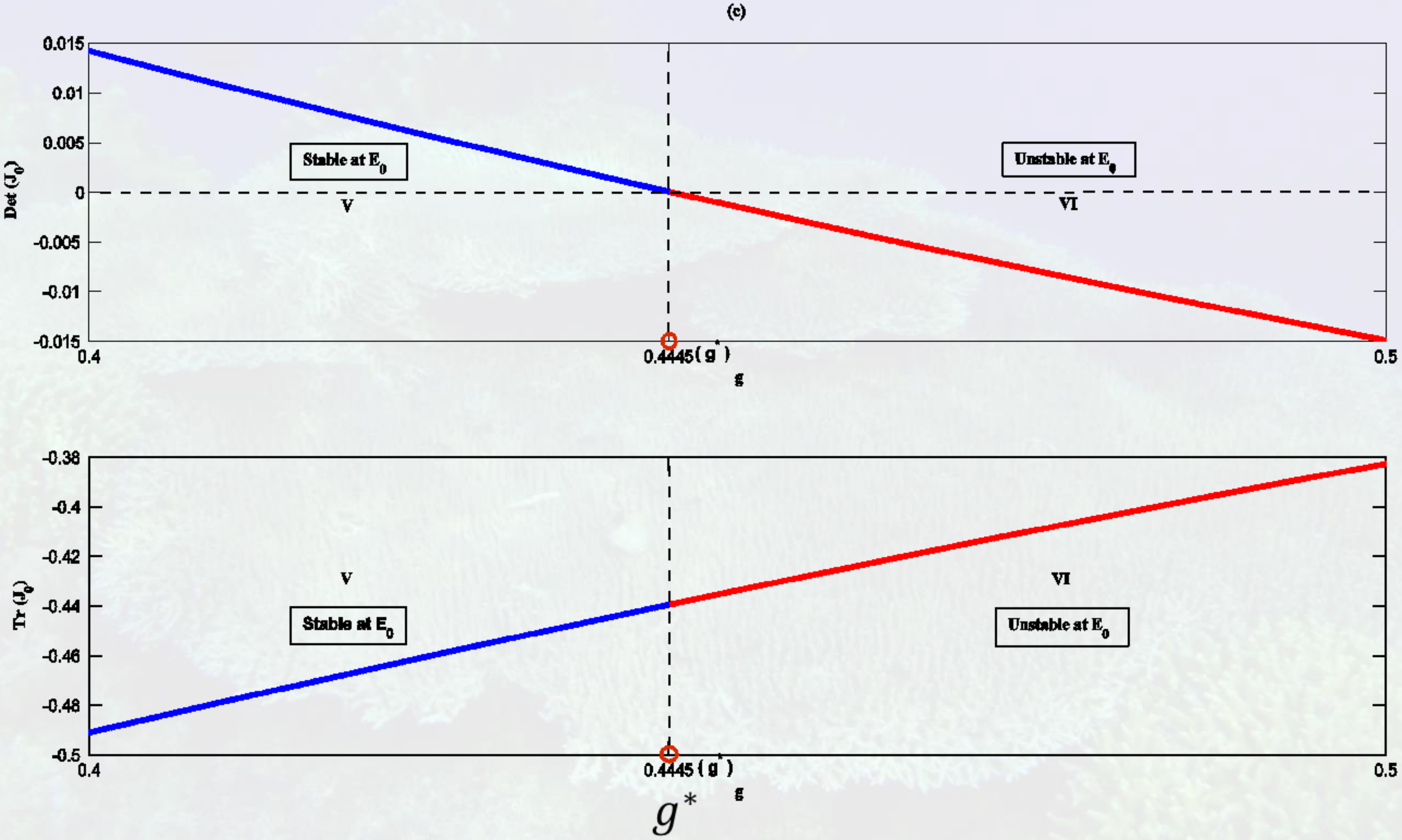
Region III ($\gamma = 0.45$)

Saddle − node bifurcation at g_*



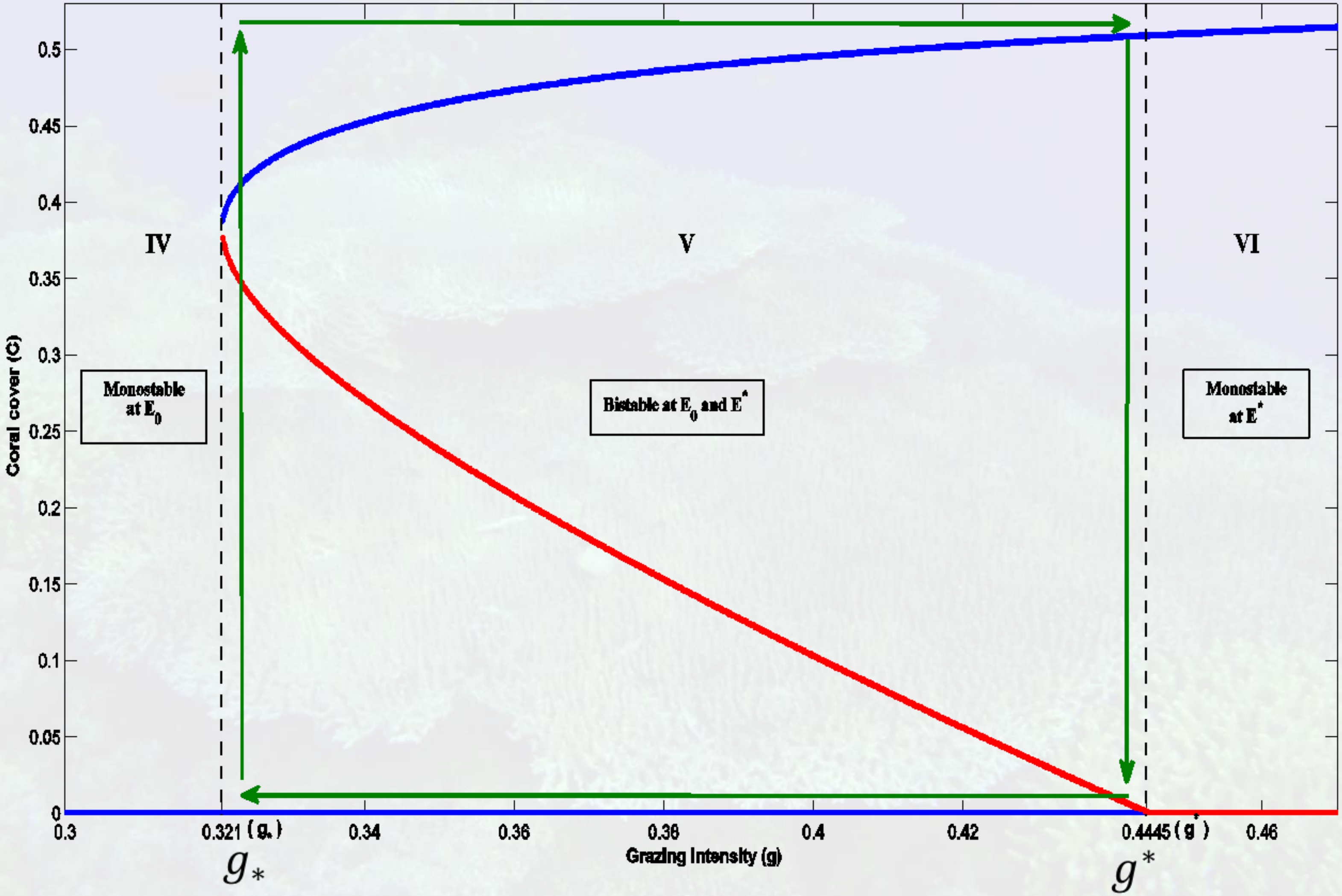
(a) At $g_*, Det(J^*) = 0$ *and* $Tr(J^*) < 0$ *with stability at* E^* *for* $g > g_* = 0.32102$ *and non − existence of* E^* *when* $g < g_*$.

Transcritical bifurcation at g^*



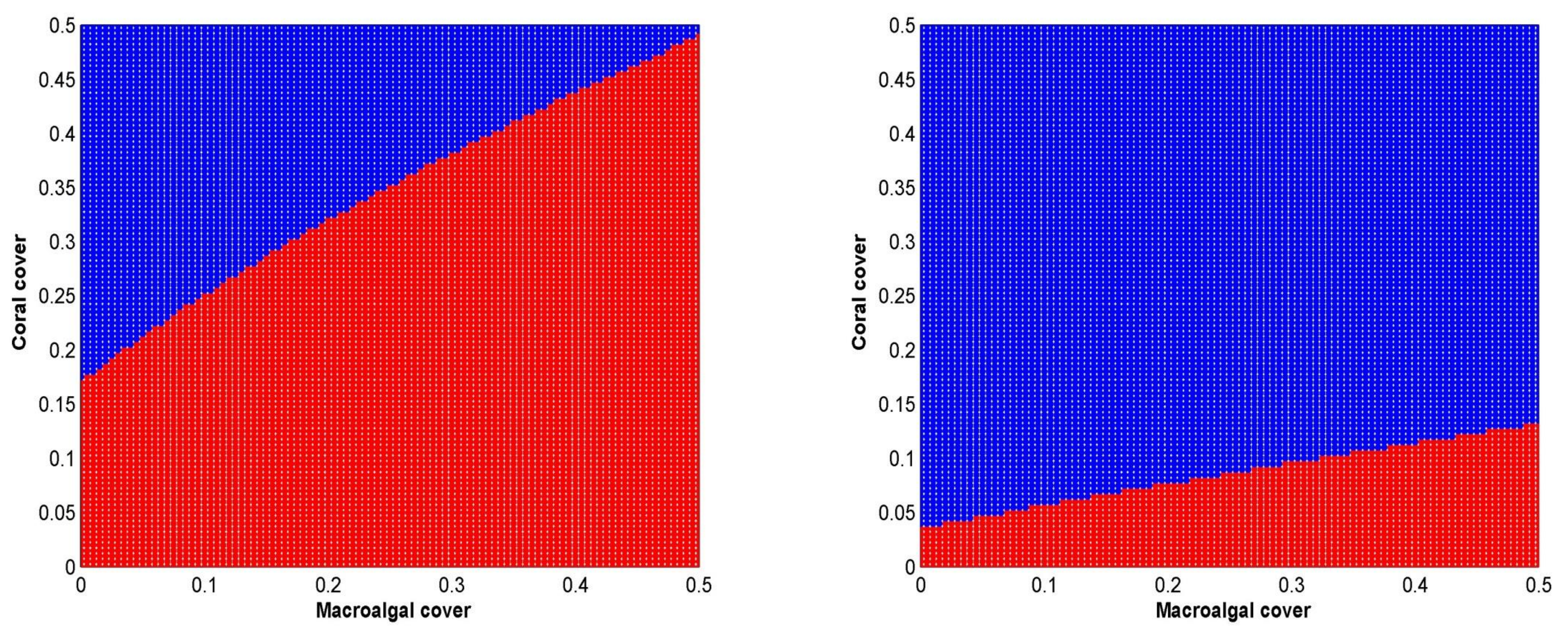
(b) $At\ g^*, Det(J_0) = 0\ and\ Tr(J_0) < 0\ with\ instability\ at\ E_0\ for$
$g > g^* = 0.4445\ and\ stability\ at\ E_0\ when\ g < g^*.$

Bifurcation diagram of g vs. the equilibrium value of coral cover.



Hysteresis will result in with low-intensity grazing followed by an increase in the grazing intensity above a critical threshold g^*

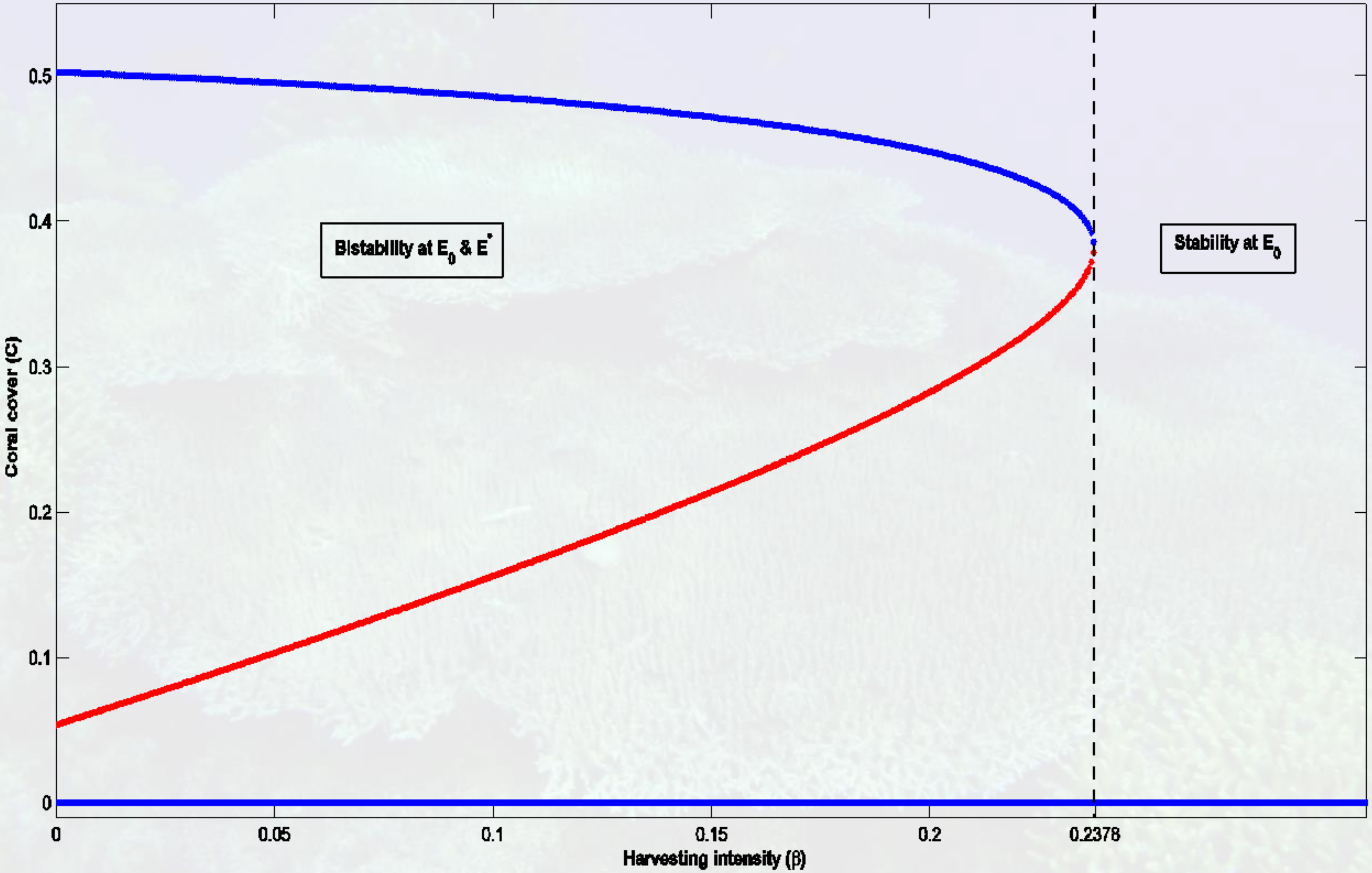
Basin of attraction for E_0 and E^*



(a)The basin of attraction for E^*(blue) and E_0 (red) with g = 0.33.

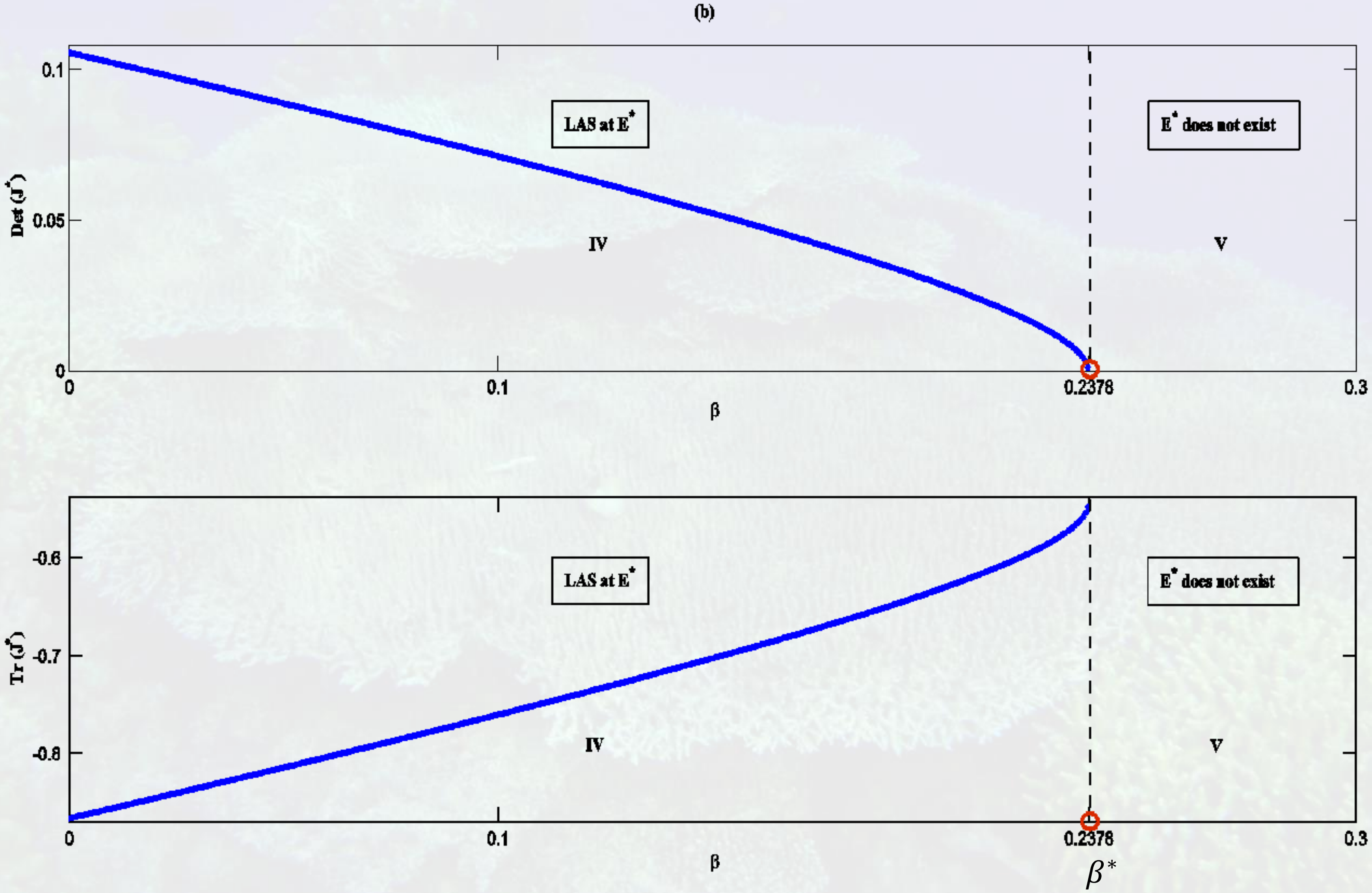
(b)The basin of attraction for E^* (blue) and E_0 (red) with g = 0.4.

Bifurcation diagram of β vs. the equilibrium value of coral cover.

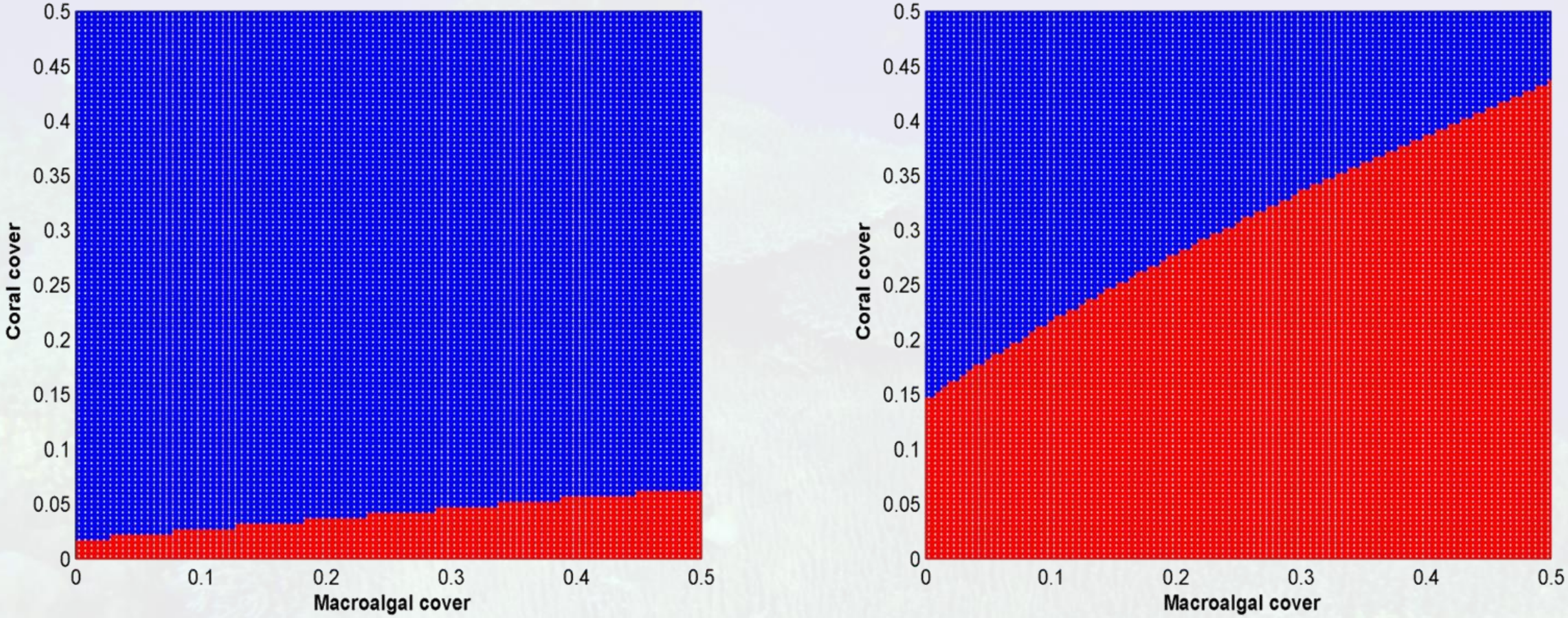


Hysteresis will result in with low harvest level followed by an increase in the harvest level above a critical threshold β^*

Saddle-node bifurcation at β^*



Basin of attraction for E_0 and E^*



(a)The basin of attraction for E^*(blue) and E_0 (red) with $\beta = 0$ (no harvesting).

(b)The basin of attraction for E^* (blue) and E_0 (red) with $\beta = 0.2$.

System with delay

We analyze the dynamics of coral reefs by assuming that the recovery of algal turf after being grazed by herbivores is not instantaneous but will be mediated by some discrete time lag τ_1. Further, we assume that macroalgae liberate toxic substances at a time lag τ_2, required for its maturity.

$$\begin{aligned}
\frac{dM}{dt} &= M(\alpha C - d_1) + T(aM + b) - \frac{g(1-\beta)M(t-\tau_1)}{M(t-\tau_1) + T(t-\tau_1)} \\
\frac{dC}{dt} &= C\{rT - \alpha M - \gamma M(t-\tau_2) - d_2\} \qquad (3) \\
\frac{dT}{dt} &= \frac{g(1-\beta)M(t-\tau_1)}{M(t-\tau_1) + T(t-\tau_1)} + d_1 M + C\{d_2 + \gamma M(t-\tau_2)\} - T(aM + rC + b)
\end{aligned}$$

Since $M + C + T = 1$, system (3) reduces to:

$$\begin{aligned}
\frac{dM}{dt} &= M(\alpha C - d_1) + (aM + b)(1 - M - C) - \frac{g(1-\beta)M(t-\tau_1)}{1 - C(t-\tau_1)} \qquad (4) \\
\frac{dC}{dt} &= C\{r(1 - M - C) - \alpha M - \gamma M(t-\tau_2) - d_2\}
\end{aligned}$$

with the initial conditions $M(t) = \phi_1(t) \geq 0, C(t) \geq \phi_2(t) \geq 0, -\tau \leq t \leq 0$, where $\tau = \max\{\tau_1, \tau_2\}, \Phi = (\phi_1, \phi_2) \in C([-\tau, 0], R^3_{+0})$, the Banach space of continuous functions, mapping the interval $(-\tau, 0)$ into R^2_{+0}, where we define $R^2_{+0} = \{(M, C) : M, C \geq 0\}$.

System with delay contd.

For $0 \leq t \leq \min\{\tau_1, \tau_2\}$, we have

$$\begin{aligned}\frac{dM}{dt} &= M(t)\{\alpha C(t) - d_1\} + \{aM(t) + b\}\{1 - M(t) - C(t)\} - \frac{g(1-\beta)\phi_1(t-\tau_1)}{1-\phi_2(t-\tau_1)} \\ \frac{dC}{dt} &= C(t)\left[r\{1 - M(t) - C(t)\} - \alpha M(t) - \gamma\phi_1(t-\tau_2) - d_2\right\}\end{aligned}$$

Therefore, for $0 \leq t \leq \min\{\tau_1, \tau_2\}$, $\frac{dM}{dt} > 0$ implies $\phi(t-\tau_1) < l_1\{1 - \phi_2(t-\tau_1)\}$ and $\frac{dC}{dt} > 0$ implies $\phi_1(t-\tau_2) < l_2(t)$, where $l_1(t) = \frac{M(t)\{\alpha C(t)-d_1\}+a\{M(t)+b\}\{1-M(t)-C(t)\}}{g(1-\beta)}$ and $l_2(t) = \frac{r\{1-M(t)-C(t)\}-\alpha M(t)-d_2}{\gamma}$.

Thus, the system is well posed in $-\tau \leq s \leq 0$ if $0 \leq M(s) = \phi_1(s) \leq \max\{l_1(s+\tau_1)\{1-\phi_2(s)\}, l_2(s+\tau_2)\}$ and $0 < C(s) = \phi_2(s)$.

The characteristic equation of the system (3) at E^* is

$D(\lambda, \tau_1, \tau_2) = \lambda^2 + \bar{A}\lambda + \bar{B} + e^{-\lambda\tau_1}\bar{C} + e^{-\lambda\tau_2}\bar{D} + \bar{E}e^{-\lambda(\tau_1+\tau_2)} = 0$, where $\bar{A} = -a_{11} - a_{22}$, $\bar{B} = a_{11}a_{22} - a_{12}a_{21}$, $\bar{C}_2 = -a_{13}$, $\bar{D} = a_{22}a_{13} - a_{14}a_{21}$, $\bar{E} = -a_{12}a_{23}$, $\bar{F} = -a_{14}a_{23}$, $a_{11} = \alpha C^* - d_1 - (aM^* + b) + a(1 - M^* - C^*)$, $a_12 = \alpha M^* - (aM^* + b)$, $a_{13} = -\frac{g(1-\beta)}{1-C^*}$, $a_{14} = -\frac{g(1-\beta)M^*}{(1-C^*)^2}$, $a_{21} = -(r+\alpha)C^*$, $a_{22} = r(1 - M^* - 2C^*) - (\alpha+\gamma)M^* - d_2$ and $a_{23} = \gamma C^*$.

System with $\tau_1 > 0$ and $\tau_2 = 0$

We now consider the case in which the recovery of algal turf after being grazed by herbivores is mediated by some discrete time lag τ_1 and an instantaneous macroalgal-toxic liberation. The system (3) reduces to

$$\begin{aligned} \frac{dM}{dt} &= M(\alpha C - d_1) + (aM + b)(1 - M - C) - \frac{g(1-\beta)M(t-\tau_1)}{1 - C(t-\tau_1)} \\ \frac{dC}{dt} &= C\{r(1 - M - C) - (\alpha + \gamma)M - d_2\} \end{aligned} \tag{4}$$

with the initial conditions $M(t) = \phi_1(t) \geq 0, C(t) = \phi_2(t) \geq 0, -\tau_1 \leq t \leq 0$ and $\phi_i(0) > 0$ $(i = 1, 2)$.

The characteristic equation of the system (4) at E^* is $\lambda^2 + \lambda A_1 + B - e^{-\lambda\tau_1}(C_1 + \lambda D_1) = 0$, where $A_1 = \bar{A}, B_1 = \bar{B} - \bar{E}, C_1 = -\bar{F} - \bar{D}$ and $D_1 = -\bar{C}$.

System with $\tau_1 > 0$ and $\tau_2 = 0$ (contd.)

Lemma 4.3. *Assume that the conditions of Lemma 3.2 are satisfied. If either (i)* $B_1^2 < C_1^2$ *or (ii)* $D_1^2 + 2B_1 - A_1^2 = 2\sqrt{B_1^2 - C_1^2} > 0$ *holds, a Hopf bifurcation occurs as* τ_1 *crosses* τ_1^+, *where* $\tau_1^+ = \frac{1}{\omega_+} \tan^{-1}\left\{\frac{\omega_+ D_1(B_1-\omega_+^2) - \omega_+ A_1 C_1}{\omega_+^2 A_1 D_1 + C_1(B_1 - \omega_+^2)}\right\}$.

Lemma 4.4. *Assume that the conditions of Lemma 3.2 are satisfied. If* $D_1^2 + 2B_1 - A_1^2 > 2\sqrt{B_1^2 - C_1^2} > 0$ *holds, then there exists a positive integer* k *such that there are* k *switches from stability to instability and from instability to stability. Therefore, Hopf bifurcation occurs as* τ_1 *crosses* $\tau_{1_n}^{\pm}$, *where* $\tau_{1_n}^{\pm} = \frac{1}{\omega_\pm} \tan^{-1}\left\{\frac{\omega_\pm D_1(B_1-\omega_\pm^2) - \omega_\pm A_1 C_1}{\omega_\pm^2 A_1 D_1 + C_1(B_1 - \omega_\pm^2)}\right\} + \frac{n\pi}{\omega_\pm}$, $(n = 0, 1, 2, \ldots, k)$.

System with $\tau_1 = 0$ and $\tau_2 > 0$

We now consider the case of instantaneous recovery of algal turf after being grazed by herbivores but a discrete time lag τ_2 for macroalgal-toxic liberation.

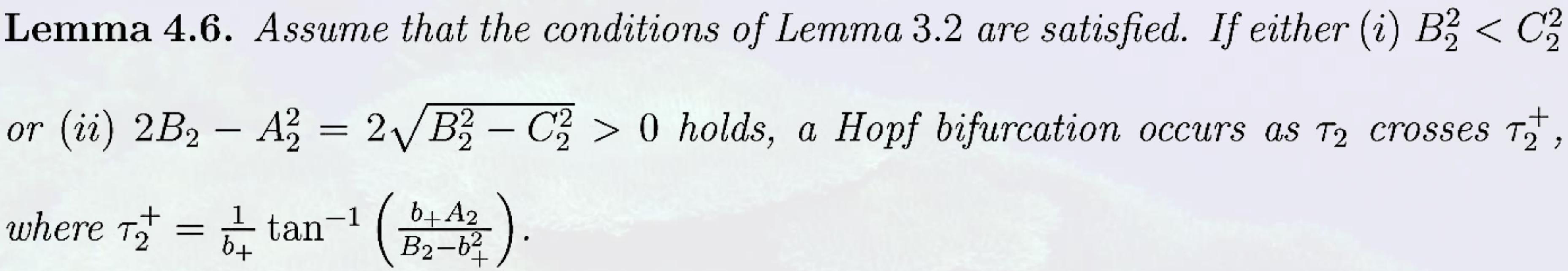
The system (3) reduces to

$$\begin{aligned}\frac{dM}{dt} &= M\left\{\alpha C - \frac{g(1-\beta)}{1-C} - d_1\right\} + (aM+b)(1-M-C) \\ \frac{dC}{dt} &= C\left\{r(1-M-C) - \alpha M + \gamma M(t-\tau_2) - d_2\right\}\end{aligned} \tag{7}$$

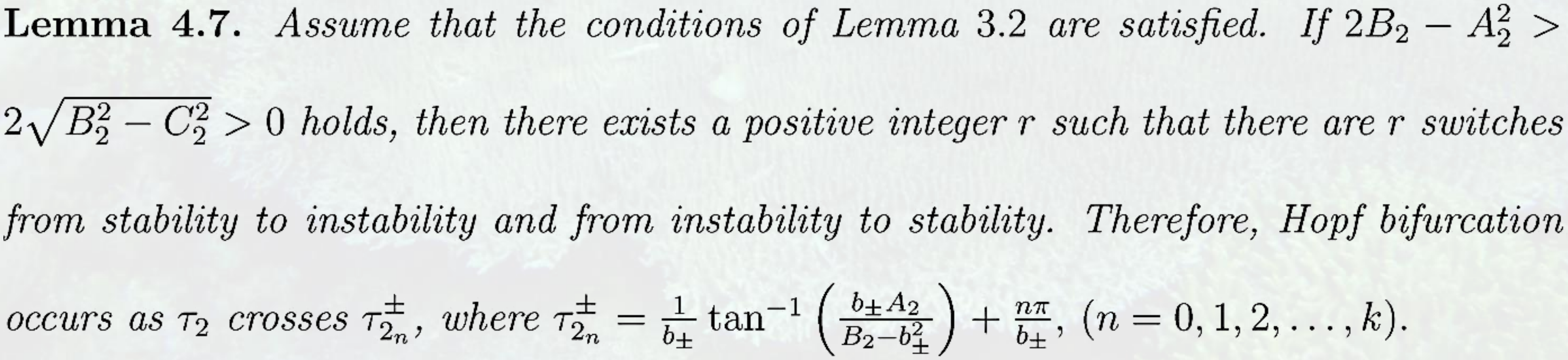
with the initial conditions $M(t) \geq 0, C(t) = \phi_2(t) \geq 0, -\tau_2 \leq t \leq 0$ and $\phi_2(0) > 0$.

The characteristic equation of the system (7) at E^* is $\lambda^2 + \lambda A_2 + B_2 - C_2 e^{-\lambda\tau_2} = 0$, where $A_2 = \bar{A} + \bar{C}, B_2 = \bar{B} + \bar{D}$ and $C_2 = -(\bar{E} + \bar{F})$.

System with $\tau_1 = 0$ and $\tau_2 > 0$ (contd.)



Lemma 4.6. *Assume that the conditions of Lemma* 3.2 *are satisfied. If either* (*i*) $B_2^2 < C_2^2$ *or* (*ii*) $2B_2 - A_2^2 = 2\sqrt{B_2^2 - C_2^2} > 0$ *holds, a Hopf bifurcation occurs as* τ_2 *crosses* τ_2^+, *where* $\tau_2^+ = \frac{1}{b_+}\tan^{-1}\left(\frac{b_+ A_2}{B_2 - b_+^2}\right)$.



Lemma 4.7. *Assume that the conditions of Lemma* 3.2 *are satisfied. If* $2B_2 - A_2^2 > 2\sqrt{B_2^2 - C_2^2} > 0$ *holds, then there exists a positive integer* r *such that there are* r *switches from stability to instability and from instability to stability. Therefore, Hopf bifurcation occurs as* τ_2 *crosses* $\tau_{2_n}^{\pm}$, *where* $\tau_{2_n}^{\pm} = \frac{1}{b_\pm}\tan^{-1}\left(\frac{b_\pm A_2}{B_2 - b_\pm^2}\right) + \frac{n\pi}{b_\pm}$, $(n = 0, 1, 2, \ldots, k)$.

System with $\tau_1 > 0$ and $\tau_2 > 0$

we consider $D(\lambda, \tau_1, \tau_2) = 0$ in its stable interval and regard τ_1 as a parameter.

Without any loss of generality, we assume that the conditions of Lemma 3.2 are satisfied and either (i) $B_2^2 < C_2^2$ or (ii) $2B_2 - A_2^2 = 2\sqrt{B_2^2 - C_2^2} > 0$ hold. Then the system (7) is stable for $\tau_2 \in [0, \tau_2^+)$.

Let $i\omega(\omega > 0)$ be a root of $D(\lambda, \tau_1, \tau_2) = 0$. Then $D(i\omega, \tau_1, \tau_2) = 0$ gives

$-\omega^2 + \bar{B} + \bar{E}\cos\omega\tau_2 = -(\bar{F}\cos\omega\tau_2 + \bar{D})\cos\omega\tau_1 + (\bar{F}\sin\omega\tau_2 - \omega\bar{C})\sin\omega\tau_1$ and

$\omega\bar{A} - \bar{E}\sin\omega\tau_2 = (\bar{F}\cos\omega\tau_2 + \bar{D})\sin\omega\tau_1 + (\bar{F}\sin\omega\tau_2 - \omega\bar{C})\cos\omega\tau_1.$

Squaring and adding these equations we get $\omega^4 + k_1\omega^2 + k_2\omega + k_3 = 0$, where

$k_1 = \bar{A}^2 - \bar{C}^2 - 2\bar{B} - 2\bar{E}\cos\omega\tau_2, k_2 = 2(\bar{C}\bar{F} - \bar{A}\bar{E})\sin\omega\tau_2$ and $k_3 = \bar{E}^2 + \bar{B}^2 - \bar{F}^2 - \bar{D}^2 + 2(\bar{B}\bar{E} - \bar{D}\bar{F})\cos\omega\tau_2.$

Let $G(\omega) = \omega^4 + k_1\omega^2 + k_2\omega + k_3.$

System with $\tau_1 > 0$ and $\tau_2 > 0$ (contd.)

Then if $(\bar{B}+\bar{E})^2 < (\bar{D}+\bar{F})^2$, then $G(0) < 0$. Also, $\lim_{\omega\to\infty} G(\omega) = \infty$.

We can obtain that $G(\omega) = 0$ has finite positive roots $\omega_1, \omega_2, \ldots, \omega_m$. For every fixed $\omega_i, i = 1, 2, \ldots, m$, there exists a sequence $\{\tau_{1_i}^j : j = 1, 2, 3, \ldots\}$ such that $G(\omega) = 0$ holds.

Let $\tau_1^* = \min\{\tau_{1_i}^j : i = 1, 2, \ldots, m; j = 1, 2, 3, \ldots\}$.

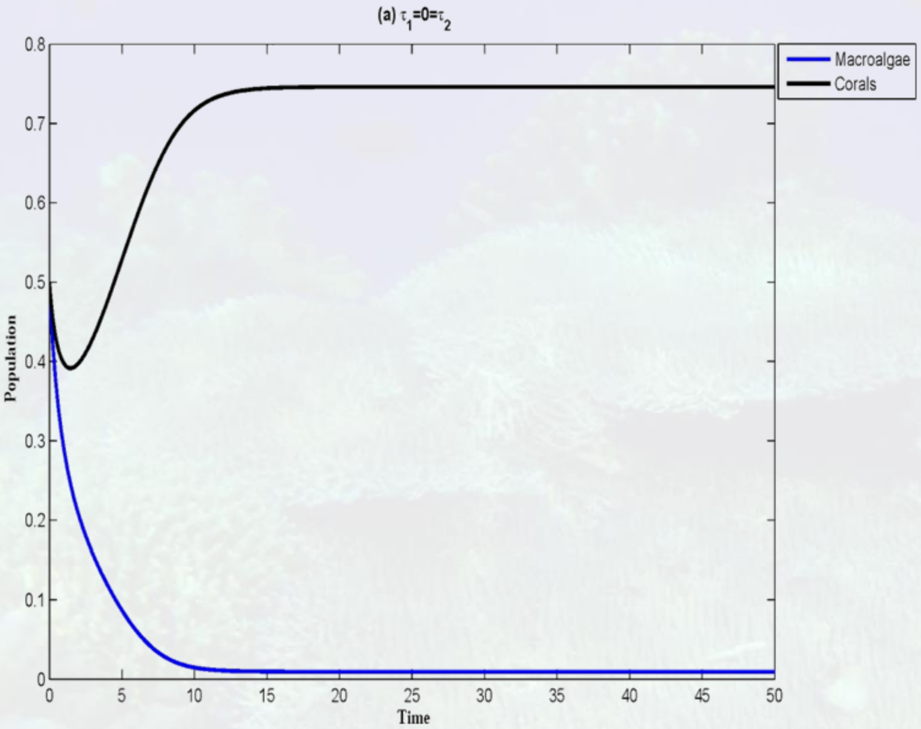
When $\tau_1 = \tau_1^*$, the equation $D(\lambda, \tau_1, \tau_2) = 0$ has a pair of purely imaginary roots $\pm i\omega^*$ for $\tau_2 \in [0, \tau_2^+)$.

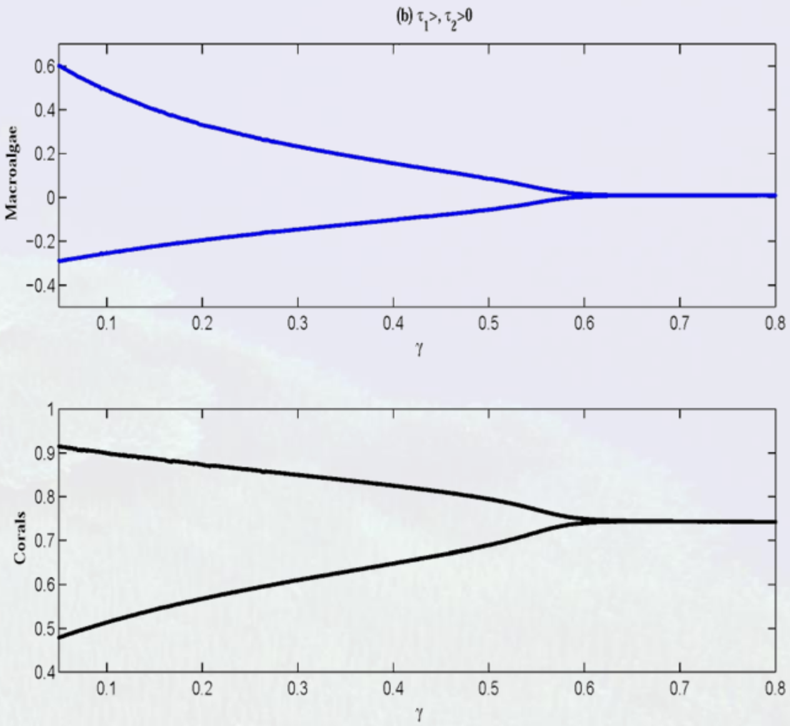
We assume that $\zeta = \left[\frac{d(Re\lambda)}{d\tau_1}\right]_{\lambda = i\omega^*} \neq 0$.

Therefore, by the general Hopf bifurcation theorem for functional differential equations, we get the following result:

Lemma 4.8. *Assume that the conditions of Lemma 3.2 are satisfied. Let* $\zeta \neq 0, (\bar{B}+\bar{E})^2 < (\bar{D}+\bar{F})^2$ *and either (i)* $B_2^2 < C_2^2$ *or (ii)* $2B_2 - A_2^2 = 2\sqrt{B_2^2 - C_2^2} > 0$ *hold for all* $\tau_2 \in [0, \tau_2^+)$. *Then* E^* *is locally asymptotically stable when* $\tau_1 \in [0, \tau_1^*)$ *and the system (3)*

System with $\tau_1 > 0$ and $\tau_2 > 0$ (contd.)

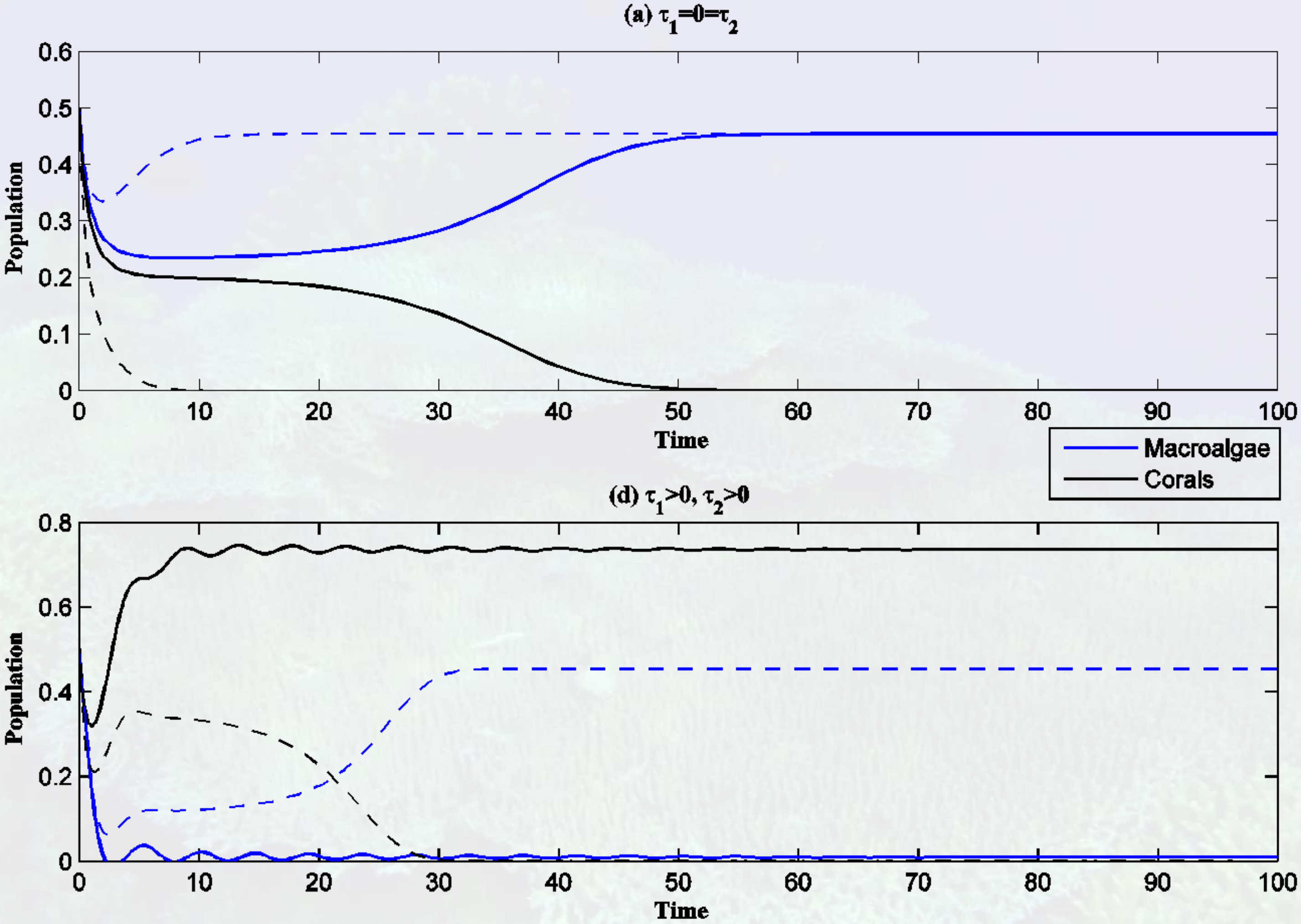




(a) For $r = 1$, other parameter values in Table 1, the system (2) is stable at coral-dominated E^*.

(b) For r = 1, τ_1 = 1.06, τ_2= 0.1, other parameter values as in Table 1, the system (3) undergoes a Hopf bifurcation as γ is increased through γ_{cr} = 0.6.

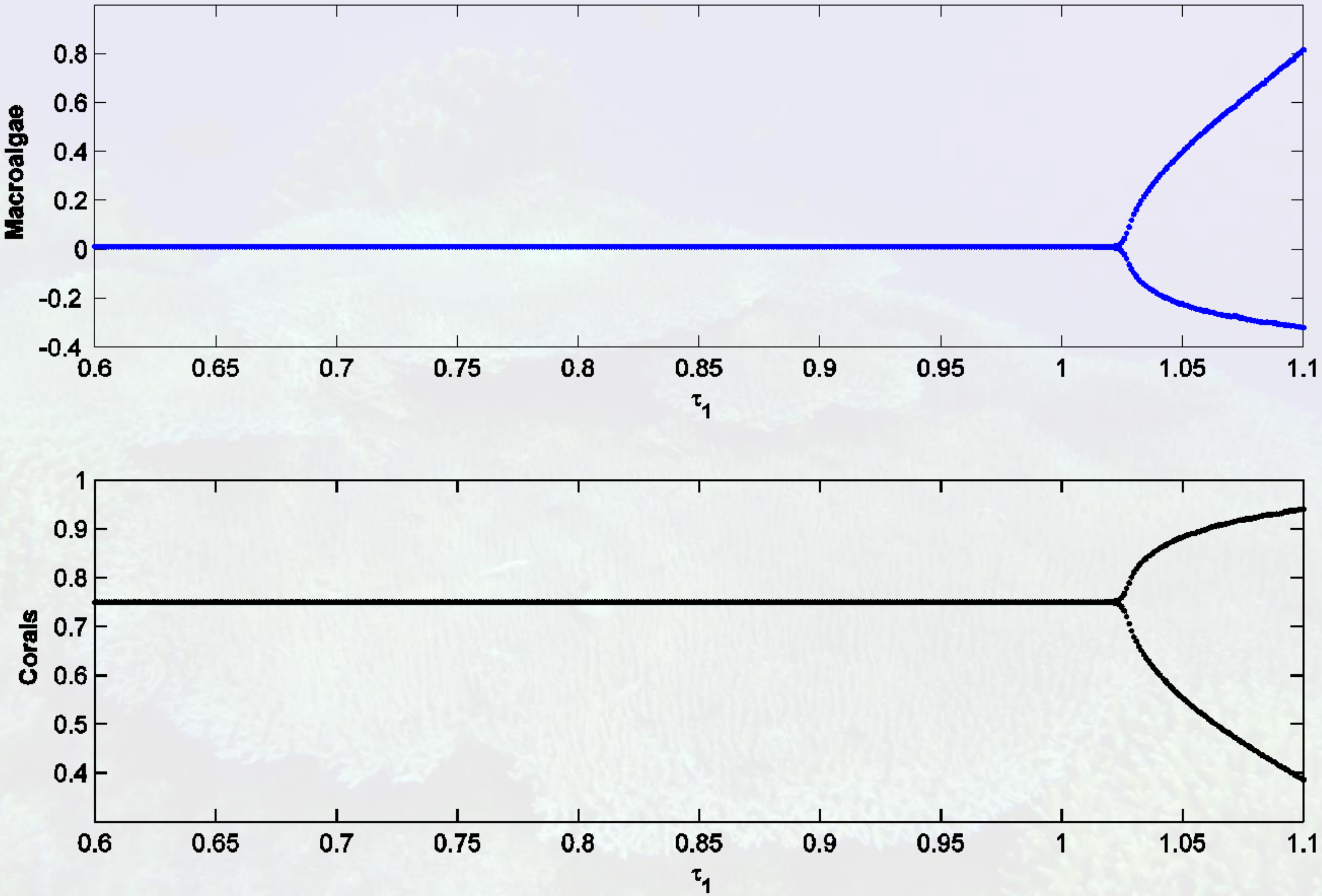
System with $\tau_1 > 0$ and $\tau_2 > 0$ (contd.)



For r = 1 and γ= 1.3, the system (2) is stable at macroalgae-dominated E_0, whereas, the system (3) with $\tau_1 = 1.06$, $\tau_2 = 0.1$, is stable at coral-dominated E^*(solid lines).

For r = 1 and γ= 2.5, the system (2) and the system (3) with $\tau_1 = 1.06$, $\tau_2 = 0.1$, both are stable at macro-dominated E_0 (dotted lines).

System with $\tau_1 > 0$ and $\tau_2 > 0$ (contd.)



For r = 1 and τ_2= 0.1, other parameter values as in Table 1, the system (3) undergoes a Hopf bifurcation as τ_1 is increased through τ_1= 1.03.

Observations

- With low macroalgal-toxicity, the system becomes stable at the coral-dominated regime. Increase of the toxicity level below a certain threshold determines two possible stable regimes depending upon the initial conditions. With high macroalgal toxicity, coral depletes completely and the system becomes stable at the coral-free equilibrium.

- With high macroalgal-toxicity, increase of grazing rate increases the resilience of the coral-dominated regime.

- With high macroalgal grazing rate by herbivores, increase of macroalgal growth rate on algal-turf increases the resilience of the coral-dominated regime.

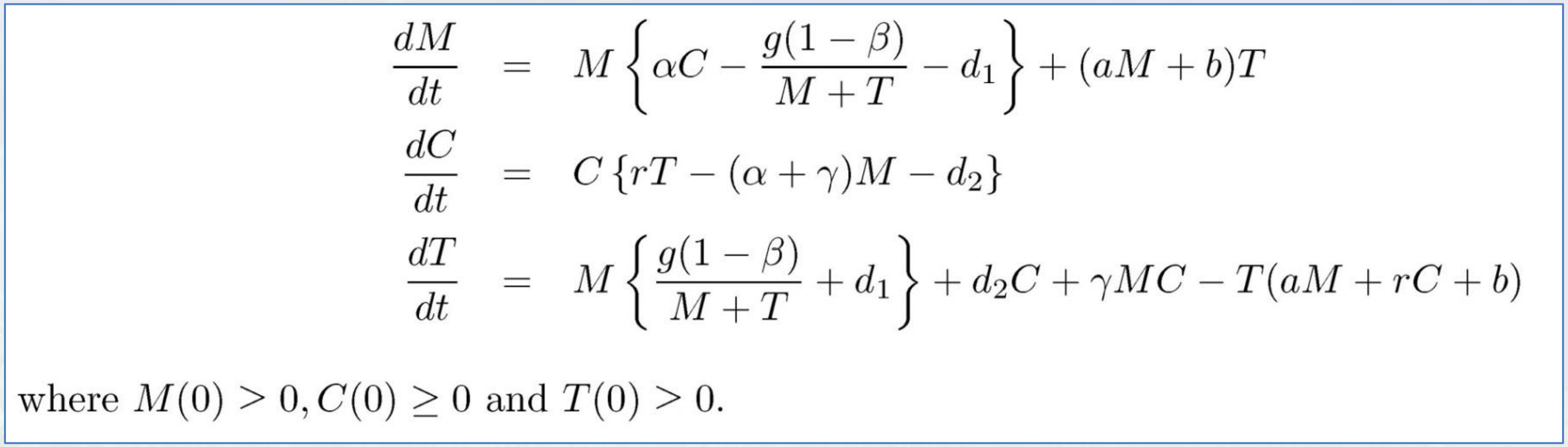
Observations (contd.)

- The system becomes stable with high growth rate of corals on turf algae even with high macroalgal-toxicity level, whereas, the system with delays becomes oscillatory when the macroalgal-toxicity level crosses a certain threshold.

- With high macroalgal-toxicity, the system becomes macroalgae-dominated and stable, whereas with the same toxicity (level below some certain threshold) the system with delays becomes coral-dominated and stable. Thus, by considering the macroalgal-recovery time lag and toxin-liberation delay, the coral-dominated system becomes more tolerant to higher toxicity level of macroalgae.

Effects of macroalgal toxicity and overfishing on the resilience of coral reefs

The Previous Model



$$\begin{aligned}
\frac{dM}{dt} &= M\left\{\alpha C - \frac{g(1-\beta)}{M+T} - d_1\right\} + (aM+b)T \\
\frac{dC}{dt} &= C\left\{rT - (\alpha+\gamma)M - d_2\right\} \\
\frac{dT}{dt} &= M\left\{\frac{g(1-\beta)}{M+T} + d_1\right\} + d_2C + \gamma MC - T(aM + rC + b)
\end{aligned}$$

where $M(0) > 0, C(0) \geq 0$ and $T(0) > 0$.

The dynamics of herbivores is not considered in this model.

Main objective

- To study the dynamics of the system in presence of herbivores in coral reefs.
- To find the resilience of the system in presence of fast-growing toxic-macroalgae and overfishing of herbivores.

Resilience

- Resilience is the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure and identity.

Some aspects of Resilience

There are three crucial aspects of resilience.

Latitude (L): the maximum amount of a system can be changed before losing its ability to recover.

Resistance (R): the ease or difficulty of changing the system.

Precariousness (Pr): how close the current state of the system is to a limit or “threshold”.

Brian Walker, *C. S. Holling*, *Stephen R. Carpenter* and *Ann Kinzig:* Resilience, adaptability and transformability in social–ecological systems. Ecol Soc 9:5 (2004) .

Modifications in the Model

Basic Assumptions:

- In absence of harvesting of *Parrotfish*, the grazing intensity of *Parrotfish* arrives at its maximum, g.

- The grazing intensity $\frac{gP}{k}$ of *Parrotfish* is proportional to the abundance of *Parrotfish* relative to its maximum carrying capacity k.

- The loss of macroalgal cover and subsequent recolonization of algal turfs due to grazing is at a rate $\frac{gMP}{k(M+T)}$

- *Parrotfish* are harvested with maximal harvesting rate h.

Modified Model

$$\begin{aligned}
\frac{dM}{dt} &= M\left\{\alpha C - \frac{gP}{k(M+T)} - d_1\right\} + (aM+b)T \\
\frac{dC}{dt} &= C\left\{rT - (\alpha+\gamma)M - d_2\right\} \\
\frac{dT}{dt} &= M\left\{\frac{gP}{k(M+T)} + d_1\right\} + d_2C + \gamma MC - T(aM+rC+b) \\
\frac{dP}{dt} &= P\left[s\left\{1 - \frac{P}{k(M+T)}\right\} - h\right]
\end{aligned}$$

where $M(0) > 0, C(0) \geq 0, T(0) > 0$ and $P(0) \geq 0$.

Bhattacharyya and Pal, DCDS-B (2017).DCDS-B 21(2), (2016)

Simplification of the model

Since $\frac{d}{dt}(M+C+T)=0$, it follows that $M(t)+C(t)+T(t)=c_0$, for all $t \geq 0$, where $c_0 = M(0) + C(0) + T(0)$.

Without any loss of generality we assume that $c_0 = 1$. Then the system reduces to

$$\begin{aligned}
\frac{dM}{dt} &= M\left\{\alpha C - \frac{gP}{k(1-C)} - d_1\right\} + (aM+b)(1-M-C) \equiv f^1 \\
\frac{dC}{dt} &= C\left\{r(1-M-C) - (\alpha+\gamma)M - d_2\right\} \equiv f^2 \\
\frac{dP}{dt} &= P\left[s\left\{1 - \frac{P}{k(1-C)}\right\} - h\right] \equiv f^3
\end{aligned}$$

where $0 < M(0) < 1, 0 \leq C(0) < 1$ and $P(0) \geq 0$.

The right-hand sides of the equations in the system reduced are smooth functions of the variables M, C, P and the parameters. As long as these quantities are non-negative, local existence and uniqueness properties hold in the positive octant.

Equilibria and their existence

(i) Coral and *Parrotfish*-free equilibrium $E_0 = (M_0, 0, 0)$, where $M_0 = \frac{a-b-d_1+\sqrt{(a+b-d_1)^2+4bd_1}}{2a}$.

E_0 always exists;

(ii) *Parrotfish*-free equilibrium $E_1 = (M_1, C_1, 0)$, where $C_1 = p + qM_1, p = 1 - \frac{d_2}{r}, q = -\frac{r+\alpha+\gamma}{r}$ and

$$M_1 = \frac{(r-d_2)\alpha - rd_1 + ad_2 + b(\alpha+\gamma) + \sqrt{\{(r-d_2)\alpha - rd_1 + ad_2 + b(\alpha+\gamma)\}^2 + 4bd_2\{(\alpha-a)(\alpha+\gamma)+r\alpha\}}}{2\{(\alpha-a)(\alpha+\gamma)+r\alpha\}}.$$

E_1 exists if $(\alpha - a)(\alpha + \gamma) + r\alpha > 0$;

(iii) coral-free equilibrium in presence of macroalgae and *Parrotfish* $E_2 = (M_2, 0, P_2)$, where $M_0 = \frac{a-b-d_1-g\left(1-\frac{h}{s}\right)+\sqrt{\left\{a-b-d_1-g\left(1-\frac{h}{s}\right)\right\}^2+4ab}}{2a}$ and $P_2 = k\left(1 - \frac{h}{s}\right)$. E_2 exists if $h < s$;

(iv) interior equilibrium $E^* = (M^*, C^*, P^*)$, where M^* is a positive root of the equation $\sum_{i=1}^{3} a_i M^{4-i} = 0$, $C^* = p_1 + q_1 M^*$ and $P^* = p_2 + q_2 M^*$, where $a_1 = \frac{k}{r^2}(r + \alpha + \gamma)[(a - \alpha)(\alpha + \gamma) - r\alpha]$, $a_2 = k\alpha q_1(1 - p_1) - kq_1(\alpha p_1 - d_1) - gq_2 + bk(1 + q_1) - ak(1 - p_1)(1 + 2q_1)$, $a_3 = k(\alpha p_1 - d_1)(1 - p_1) - gp_2 - bk(1 - p_1)(2q_1 + 1) + ak(1 - p_1)^2, a_4 = bk(1 - p_1)^2, p_1 = 1 - \frac{d_2}{r}, p_2 = \frac{k(s-h)(1-p_1)}{s}, q_1 = -\frac{r+\alpha+\gamma}{r}$ and $q_2 = -\frac{q_1 k(s-h)}{s}$. E^* exists uniquely if $r > (\alpha + \gamma)\left(\frac{a-\alpha}{\alpha}\right)$.

Stability analysis at E_0

At E_0 the eigenvalues of the Jacobian matrix of the system are $-\sqrt{(a-b-d_1)^2+4ab}$, $r-d_2-M_0(r+\alpha+\gamma)$ and $s-h$. Therefore, all the eigenvalues of the Jacobian matrix are negative if $r+\alpha+\gamma>\frac{r-d_2}{M_0}$ and $h>s$. This gives the following lemma:

Lemma

The system (2) is locally asymptotically stable at E_0 *if* $\gamma>\gamma_1$ *and* $h>s$, *where* $\gamma_1=\frac{r-d_2}{M_0}-(r+\alpha)$.

Therefore, with high macroalgal toxicity and high rate of harvesting of *Parrotfish*, the system stabilizes at macroalgae-dominated steady state with complete elimination of coral and *Parrotfish*.

Transcritical bifurcation at E_0

Lemma

If $\alpha>\frac{1}{2}\left\{a+b-d_1+\sqrt{(a+b-d_1)^2+4ad_1}\right\}$ *and* $h>s$, *the system undergoes a transcritical bifurcation at* E_0 *when* γ *crosses* γ_1.

Stability analysis at E_2

Lemma

The system is locally asymptotically stable at E_2 *if* $\gamma > \gamma_2$ *and* $h < s$, *where* $\gamma_2 = \frac{r-d_2}{M_2} - (r+\alpha)$.

Therefore, with high macroalgal toxicity and low rate of harvesting of *Parrotfish*, the system stabilizes at macroalgae-dominated steady state in presence of *Parrotfish* with complete elimination of corals.

Transcritical bifurcation at E_2

Lemma

If $h < s$ *and* $\gamma_2 \neq \frac{2r\sqrt{\left\{a-b-d_1+g\left(1-\frac{h}{s}\right)\right\}^2+4ab}}{(\alpha-a)M_2-b} - (r+\alpha)$, *the system undergoes a transcritical bifurcation at* E_2 *when* γ *crosses* γ_2.

Persistence at E^*

Lemma

The system is persistent at E^* *if* $\gamma < \min\{\gamma_1, \gamma_2\}$ *and* $h < s$.

Therefore, with low macroalgal toxicity level and low rate of harvesting of *Parrotfish*, all the organisms in the system coexists.

Stability analysis at E*

The Jacobian $J^* \equiv J(E^*)$ of the system evaluated at an interior equilibrium E^* is

$$J^* = \begin{pmatrix} -aM^* - \frac{b(1-C^*)}{M^*} & (\alpha - a)M^* - b - \frac{gM^*P^*}{k(1-C^*)^2} & -\frac{gM^*}{k(1-C^*)} \\ -(r+\alpha+\gamma)C^* & -rC^* & 0 \\ 0 & -\frac{sP^{*2}}{k(1-C^*)^2} & -\frac{sP^*}{k(1-C^*)} \end{pmatrix}$$

The characteristic equation of the Jacobian J^* of the system is $\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0$, where

$A_1 = rC^* + aM^* + \frac{b(1-C^*)}{M^*} + \frac{gP^*}{k(1-C^*)^2}$,

$A_2 = \frac{rsC^*P^*}{k(1-C^*)} + \left\{aM^* + \frac{b(1-C^*)}{M^*}\right\}\left\{rC^* + \frac{sP^*}{k(1-C^*)}\right\} + (r+\alpha+\gamma)\left\{(\alpha-a)M^*C^* - bC^* - \frac{gM^*C^*P^*}{k(1-C^*)^2}\right\}$,

$A_3 = \frac{s(r+\alpha+\gamma)C^*P^*}{k(1-C^*)}\{(\alpha-a)M^* - b\}$.

The system is locally asymptotically stable at E^* if $A_1A_2 > A_3$.

At $\alpha = a + \frac{b}{M^*} = \alpha^*$(say), we have $A_2(\alpha^*) = \frac{rsC^*P^*}{k(1-C^*)} + \left\{aM^* + \frac{b(1-C^*)}{M^*}\right\}\left\{rC^* + \frac{sP^*}{k(1-C^*)}\right\} - \frac{gM^*C^*P^*(r+\alpha^*+\gamma)}{k(1-C^*)^2}$.

Therefore, at $\alpha = \alpha^*$ if $A_2(\alpha^*) > 0$, then the Jacobian J^* of the system (2) has a simple zero eigenvalue.

Let V^* and W^* are the eigenvectors corresponding to the zero eigenvalue for J^* and J^{*T} respectively.

Then we obtain $V^* = \begin{pmatrix} \frac{-r}{r+\alpha^*+\gamma} & 1 & -P^* \end{pmatrix}^T$ and $W^* = \begin{pmatrix} 1 & -\frac{aM^* + \frac{b(1-C^*)}{M^*}}{C^*(r+\alpha^*+\gamma)} & -\frac{gM^*}{sP^*} \end{pmatrix}^T$.

Due to the complexity in the algebraic expressions involved, we will use numerical simulations to verify that $W^{*T}f_\alpha(E^*;\alpha^*) \neq 0$ and $W^{*T}[D^2f(E^*;\alpha^*)(V^*,V^*)] \neq 0$. In this case the system undergoes a saddle-node bifurcation at E^* when α crosses α^*.

Numerical Simulations

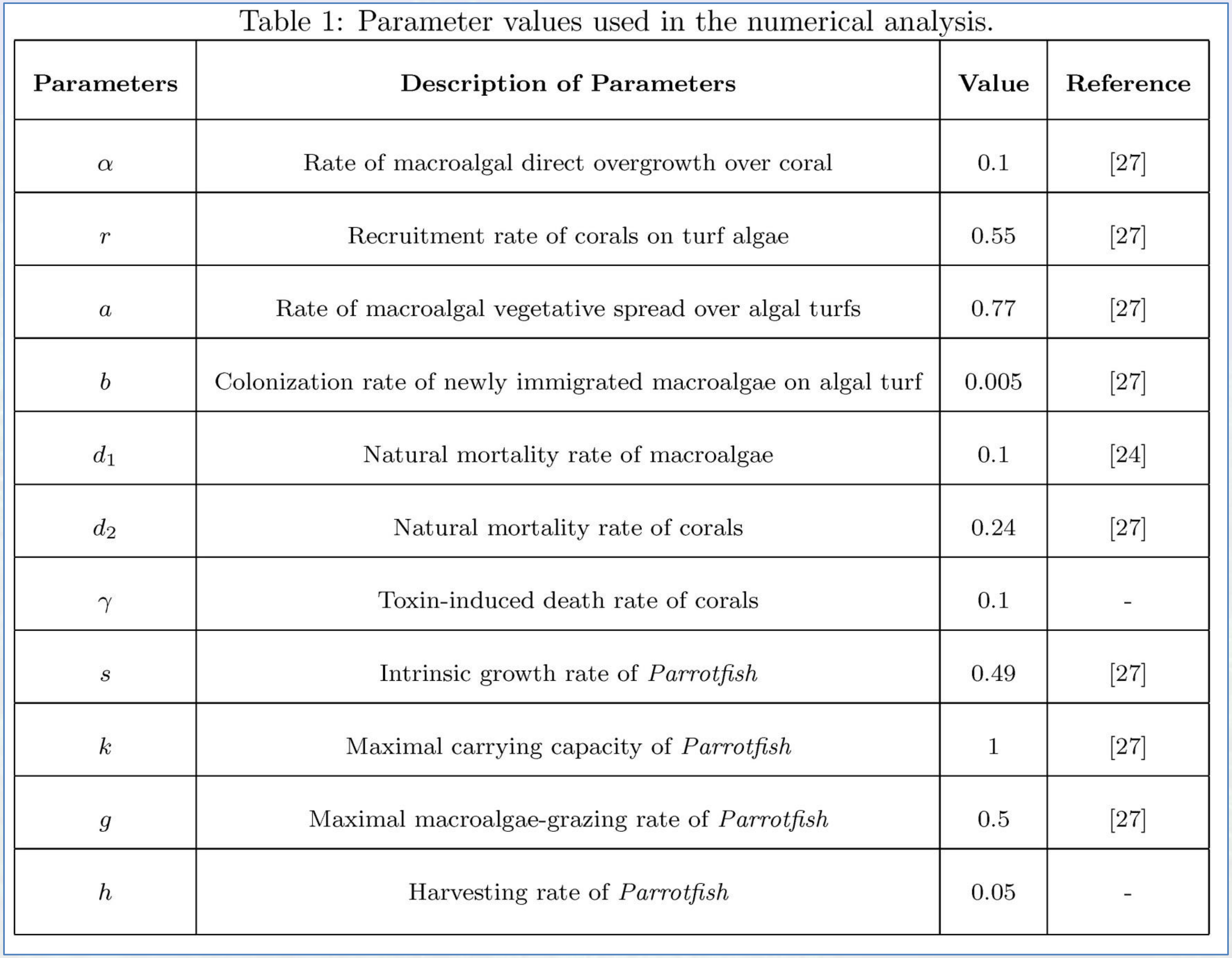
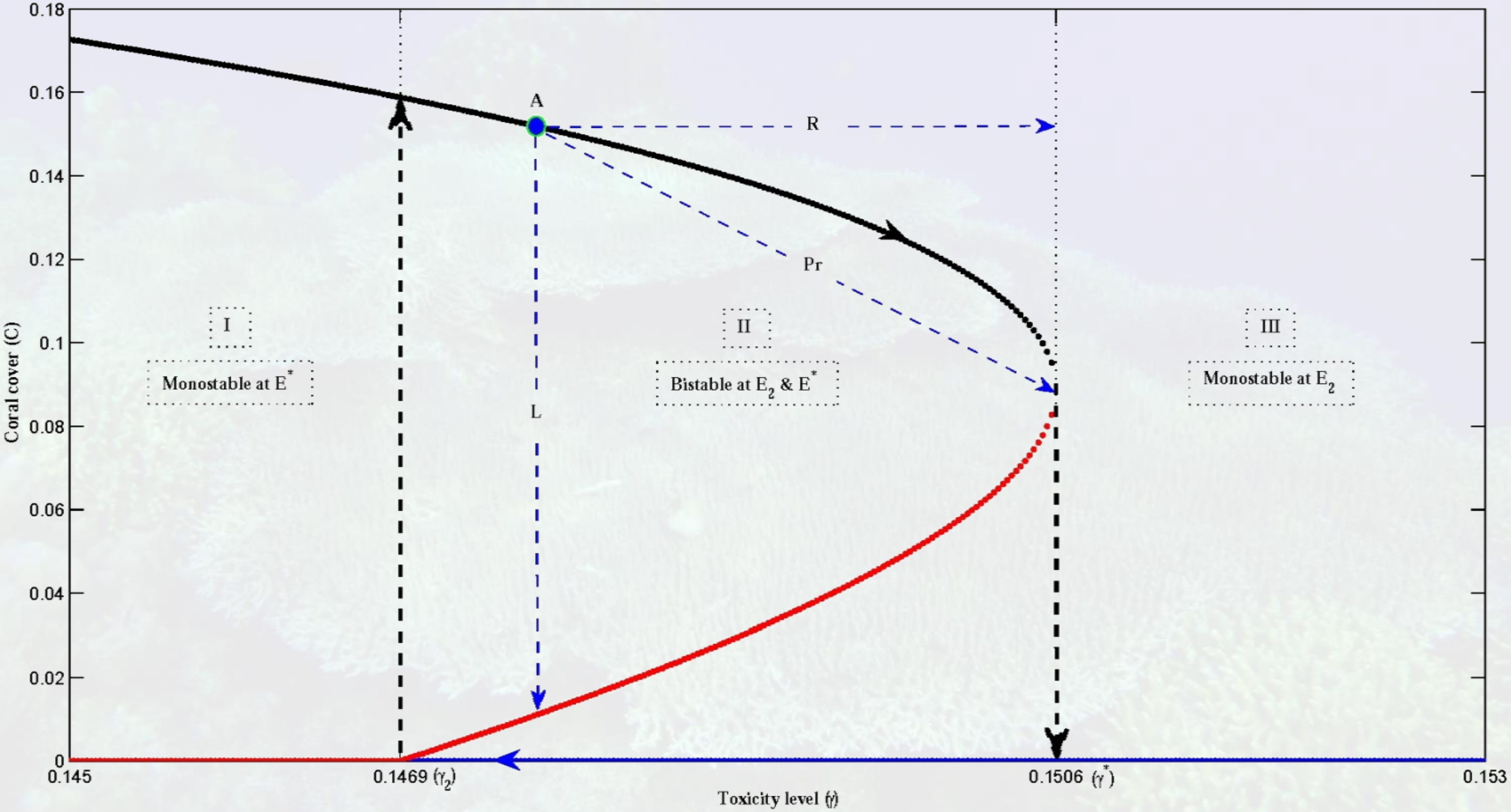


Table 1: Parameter values used in the numerical analysis.

Parameters	**Description of Parameters**	**Value**	**Reference**
α	Rate of macroalgal direct overgrowth over coral	0.1	[27]
r	Recruitment rate of corals on turf algae	0.55	[27]
a	Rate of macroalgal vegetative spread over algal turfs	0.77	[27]
b	Colonization rate of newly immigrated macroalgae on algal turf	0.005	[27]
d_1	Natural mortality rate of macroalgae	0.1	[24]
d_2	Natural mortality rate of corals	0.24	[27]
γ	Toxin-induced death rate of corals	0.1	-
s	Intrinsic growth rate of *Parrotfish*	0.49	[27]
k	Maximal carrying capacity of *Parrotfish*	1	[27]
g	Maximal macroalgae-grazing rate of *Parrotfish*	0.5	[27]
h	Harvesting rate of *Parrotfish*	0.05	-

Bifurcation diagram of γ vs. the equilibrium value of coral cover (with $h < s$)



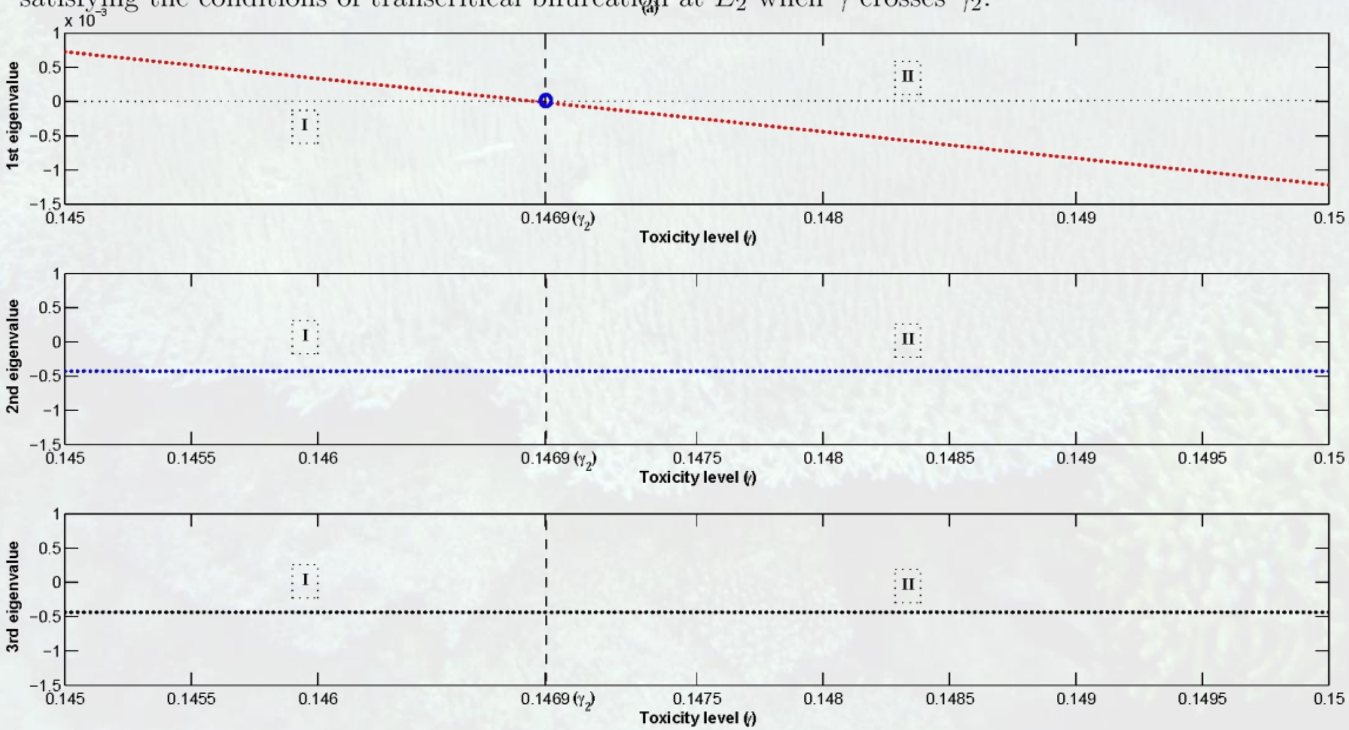
Hysteresis will result in with low toxicity level followed by an increase in the macroalgal toxicity above a critical threshold γ^*

Transcritical bifurcation at E_2 when γ crosses γ_2

At $\gamma = \gamma_2$, we have $E_2 = (0.389, 0, 0.898)$ and

$$J_2 = \begin{pmatrix} -0.4281 & -0.4853 & -0.1945 \\ 0 & 0 & 0 \\ 0 & -0.3951 & -0.44 \end{pmatrix}$$

has a simple zero eigenvalue. Also, we obtain $V_2 = \begin{pmatrix} -0.7257 & 1 & -0.8980 \end{pmatrix}^T$, $W_2 = \begin{pmatrix} 0 & 1 & 0 \end{pmatrix}^T$, $W_2^T f_\gamma(E_2;\gamma_2) = 0$, $W_2^T[Df_\gamma(E_2;\gamma_2)V_2] = -0.389 < 0$ and $W_2^T[D^2 f(E_2;\gamma_2)(V_2, V_2)] = 0.0565 > 0$, satisfying the conditions of transcritical bifurcation at E_2 when γ crosses γ_2.

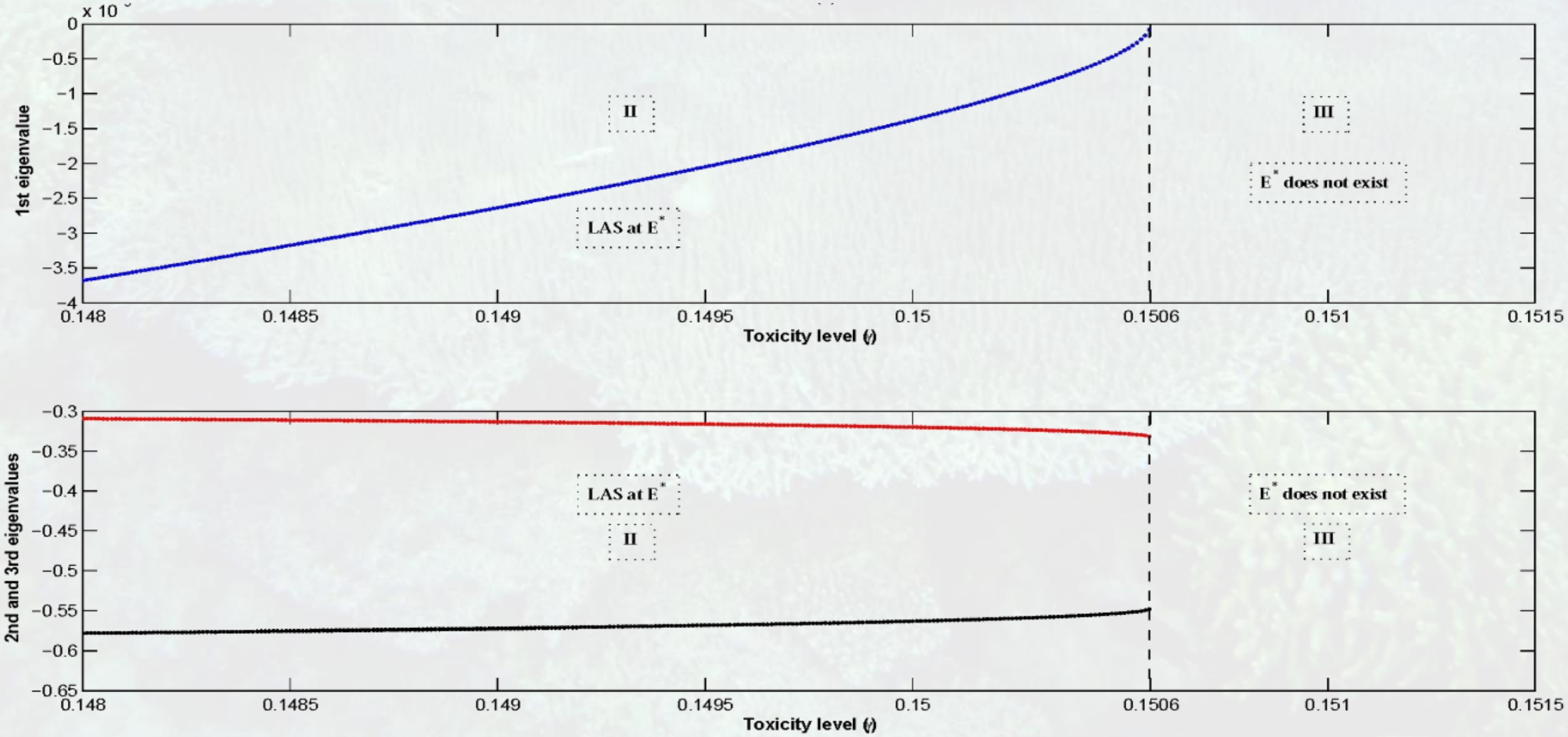


Saddle-node bifurcation at E^* when γ crosses γ^*

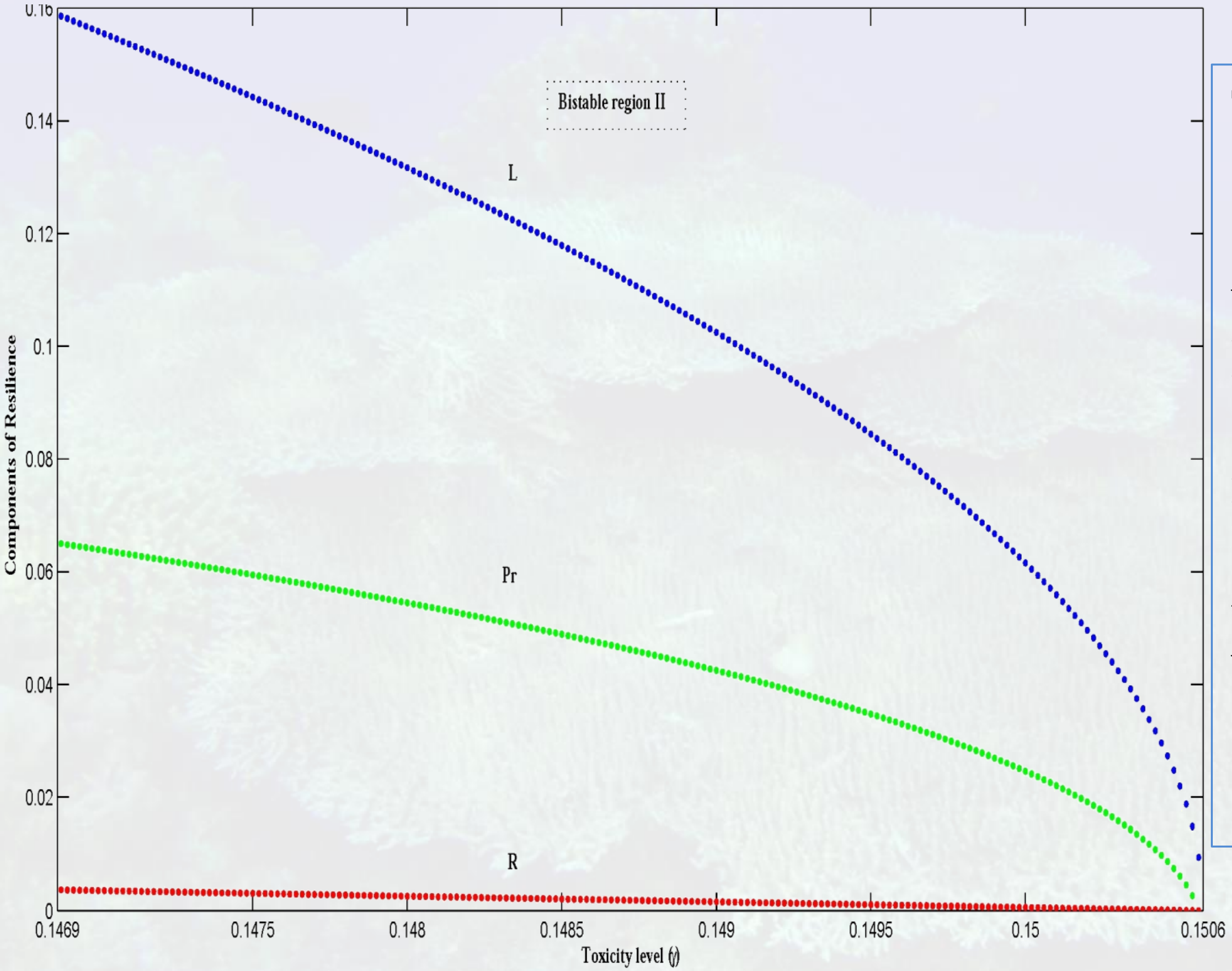
At $\gamma = \gamma^*$, we have $E^* = (0.326, 0.0891, 0.818)$ and

$$J^* = \begin{pmatrix} -0.3907 & -0.4291 & -0.179 \\ -0.0713 & -0.049 & 0 \\ 0 & -0.3951 & -0.44 \end{pmatrix}$$

with eigenvalues 0, -0.5469 and -0.3328. Also, we obtain $V^* = \begin{pmatrix} 0.8769 & 0.1256 & 0.4641 \end{pmatrix}^T$, $W^* = \begin{pmatrix} 0.4742 & -0.3852 & -0.7917 \end{pmatrix}^T$, $W^{*T} f_\gamma(E^*;\gamma^*) = 0.0112 > 0$ and $W^{*T}[D^2 f(E^*;\gamma^*)(V^*, V^*)] < 0$

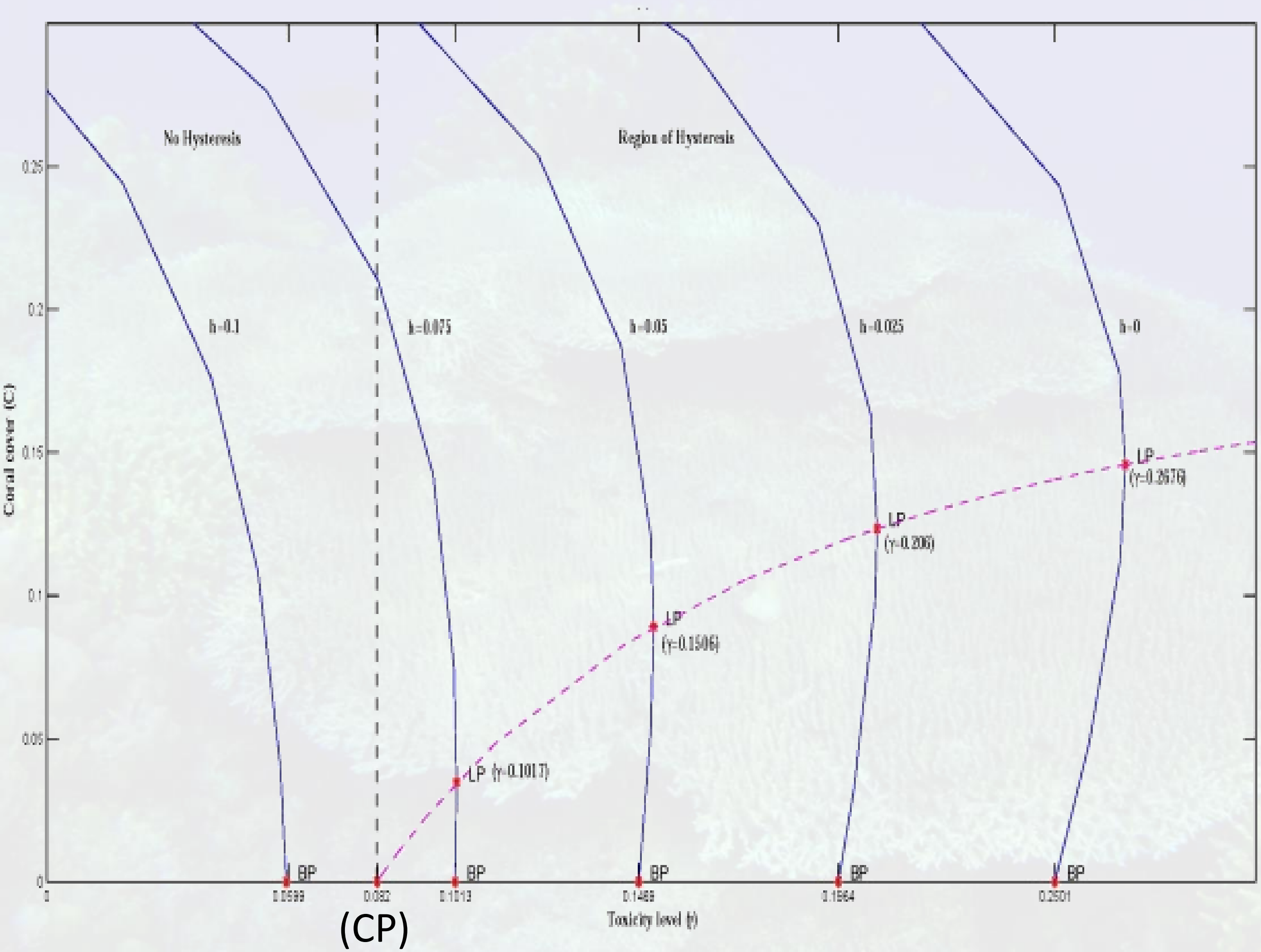


Change of Resilience at E^* due to the increase of γ



The resilience of the system at the interior equilibrium is maximum when macroalgal-toxicity level is less than γ_2 and decreases in the bistable region **II** due to the increase of macroalgal toxicity. The resilience becomes zero when macroalgal-toxicity level is increased beyond γ^*.

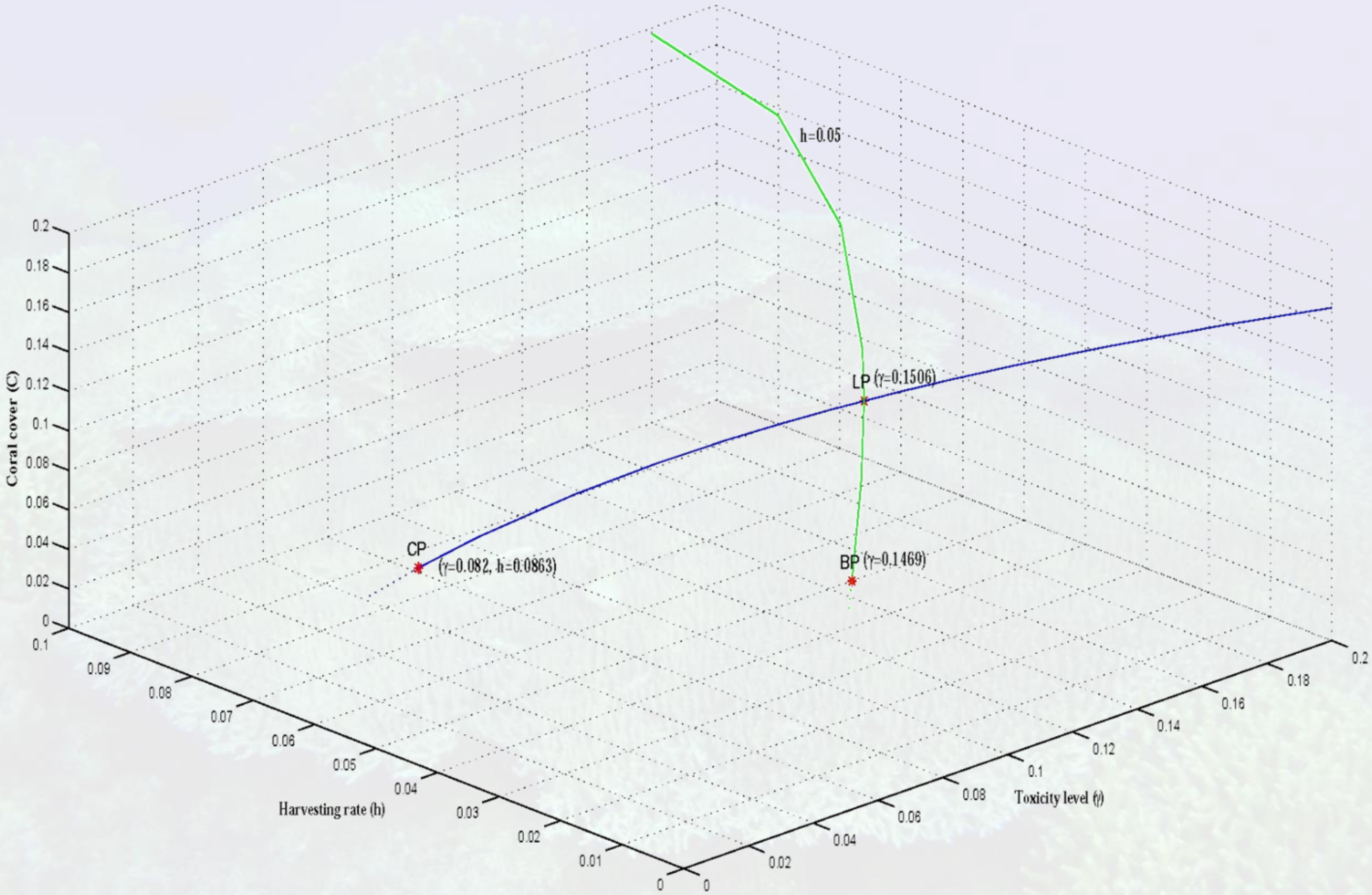
Change of Resilience at E^* due to change in γ and h



With γ and h as active parameters, the resilience of the system becomes minimum when rate of harvesting of Parrotfish is greater than $h = 0.0863$ where the saddle-node curve meets the parameter axis at, $\gamma = 0.082$ generating a cusp point (CP) at their point of intersection.

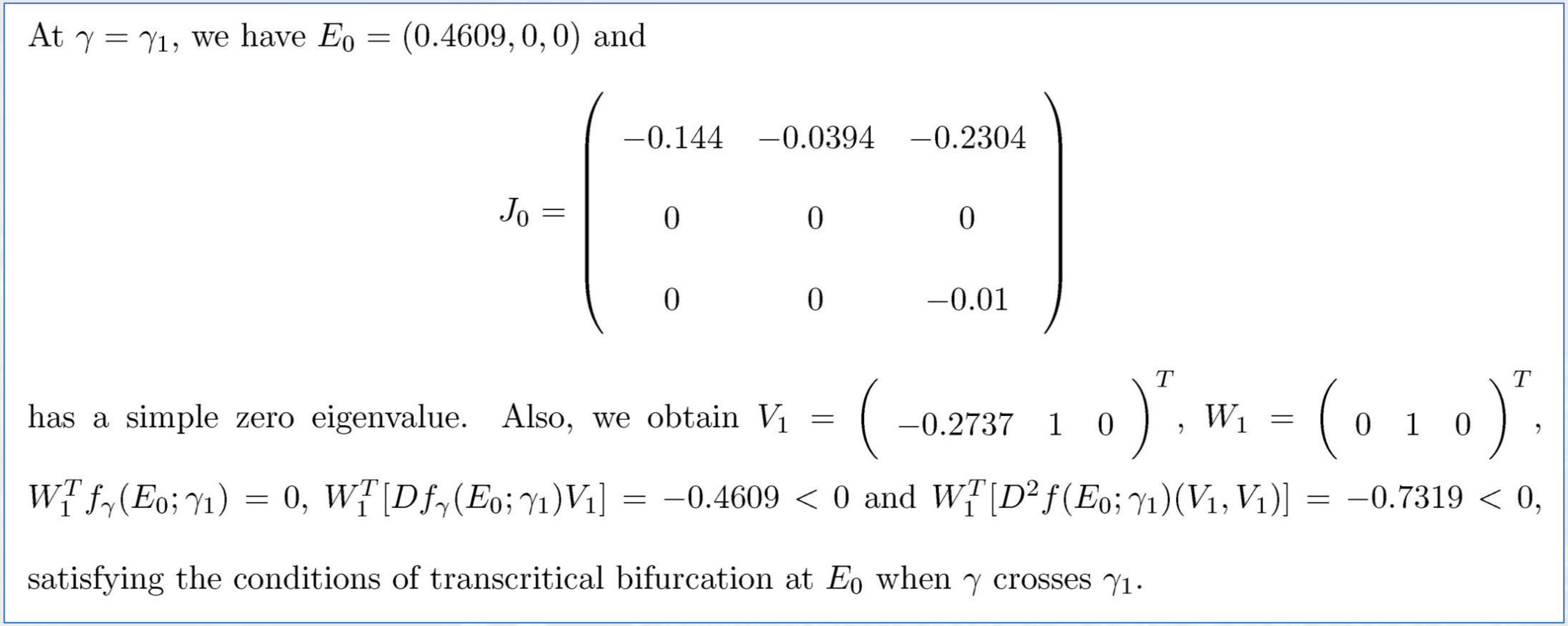
The decrease in the rate of harvesting of Parrotfish increases the latitude component of resilience due to the increase of coral cover. Also, the resistance component of resilience of coral-dominated regime is increased even with the increase of macroalgal toxicity, measured by taking the difference of the values of at the saddle-node bifurcating point (LP) and at transcritical bifurcating point (BP) for a particular value of h.

Codim2 bifurcation with γ and h as active parameters



A two-parameter bifurcation diagram with γ and h as active parameters, representing a cusp point (CP) at $(\gamma, h) = (0.082, 0.0863)$ on the saddle-node curve.

Transcritical bifurcation at E$_0$ when γ crosses γ_1

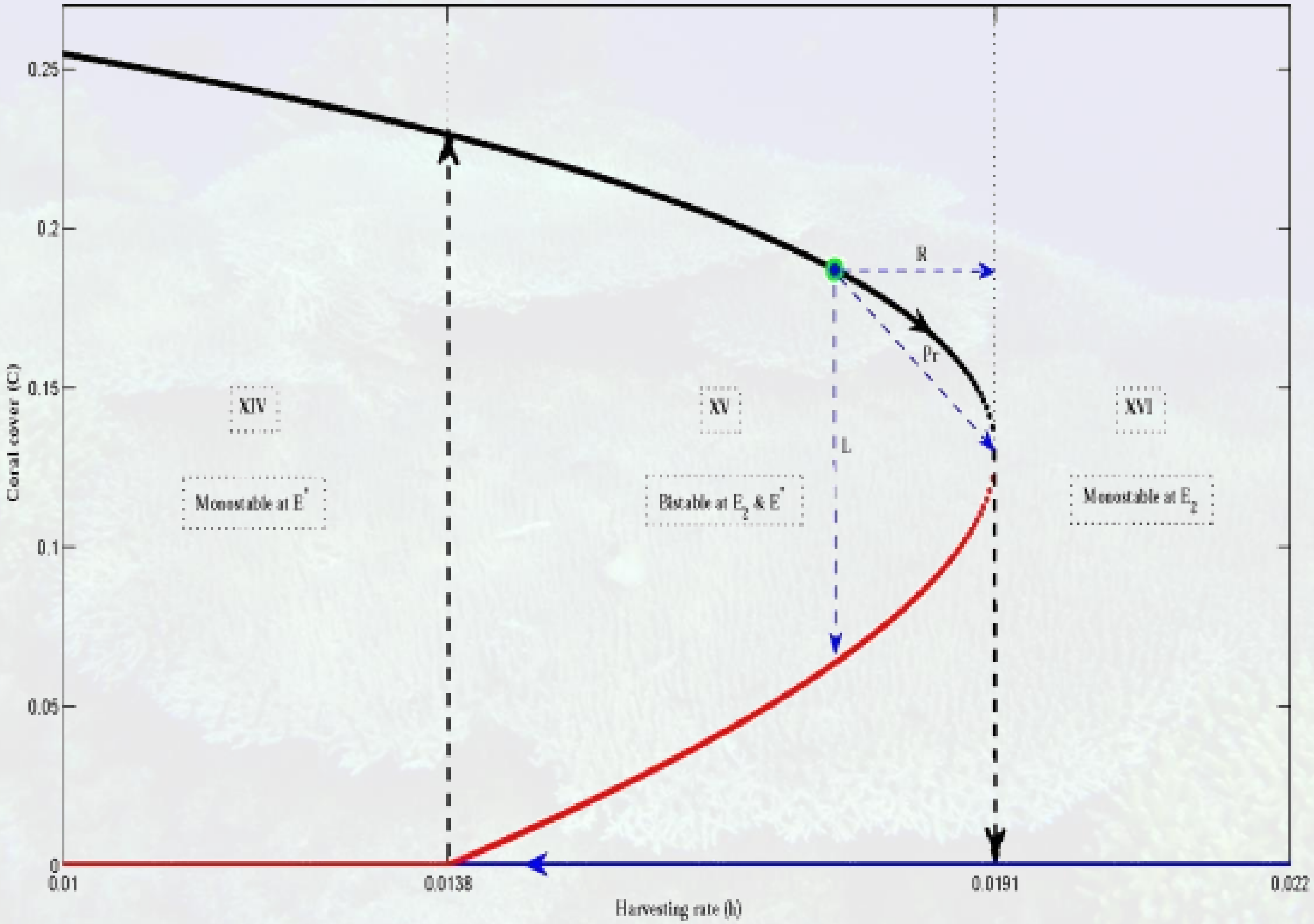


At $\gamma = \gamma_1$, we have $E_0 = (0.4609, 0, 0)$ and

$$J_0 = \begin{pmatrix} -0.144 & -0.0394 & -0.2304 \\ 0 & 0 & 0 \\ 0 & 0 & -0.01 \end{pmatrix}$$

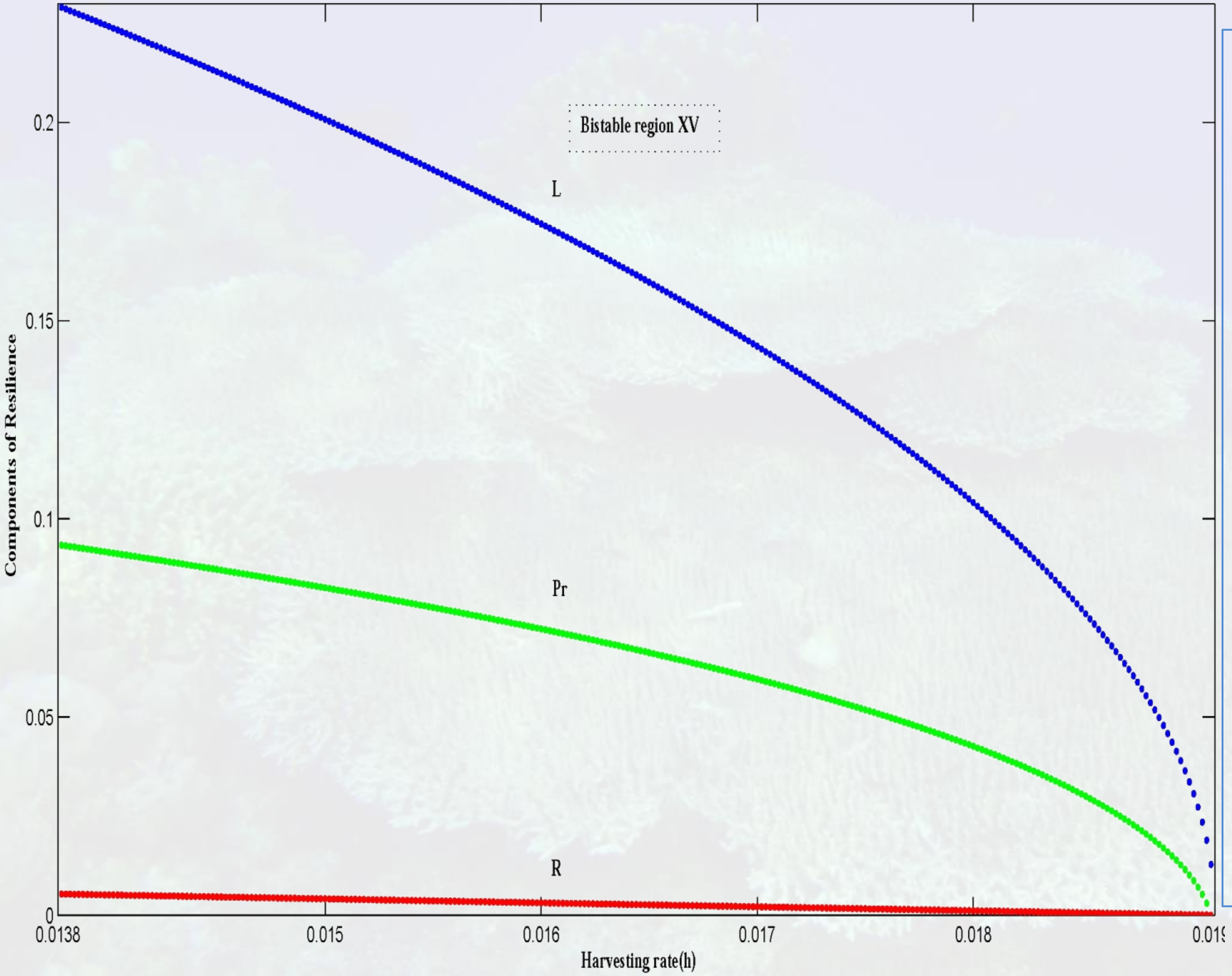
has a simple zero eigenvalue. Also, we obtain $V_1 = \begin{pmatrix} -0.2737 & 1 & 0 \end{pmatrix}^T$, $W_1 = \begin{pmatrix} 0 & 1 & 0 \end{pmatrix}^T$, $W_1^T f_\gamma(E_0; \gamma_1) = 0$, $W_1^T[Df_\gamma(E_0; \gamma_1)V_1] = -0.4609 < 0$ and $W_1^T[D^2 f(E_0; \gamma_1)(V_1, V_1)] = -0.7319 < 0$, satisfying the conditions of transcritical bifurcation at E_0 when γ crosses γ_1.

Bifurcation diagram of h vs. the equilibrium value of coral cover



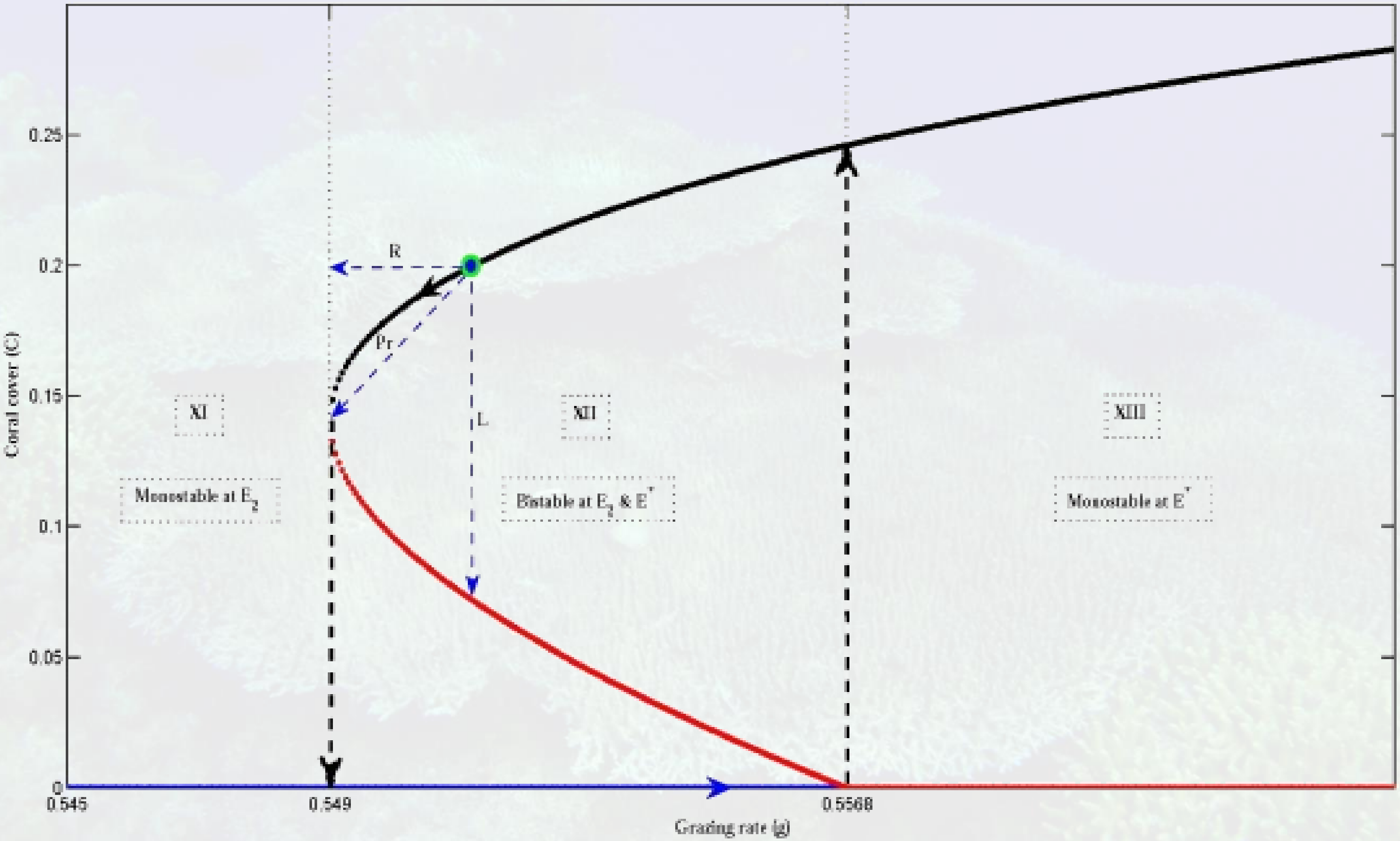
Hysteresis will result in with low harvesting rate followed by an increase in the harvesting rate above a critical threshold h^*

Change of Resilience at E^* due to the increase of h



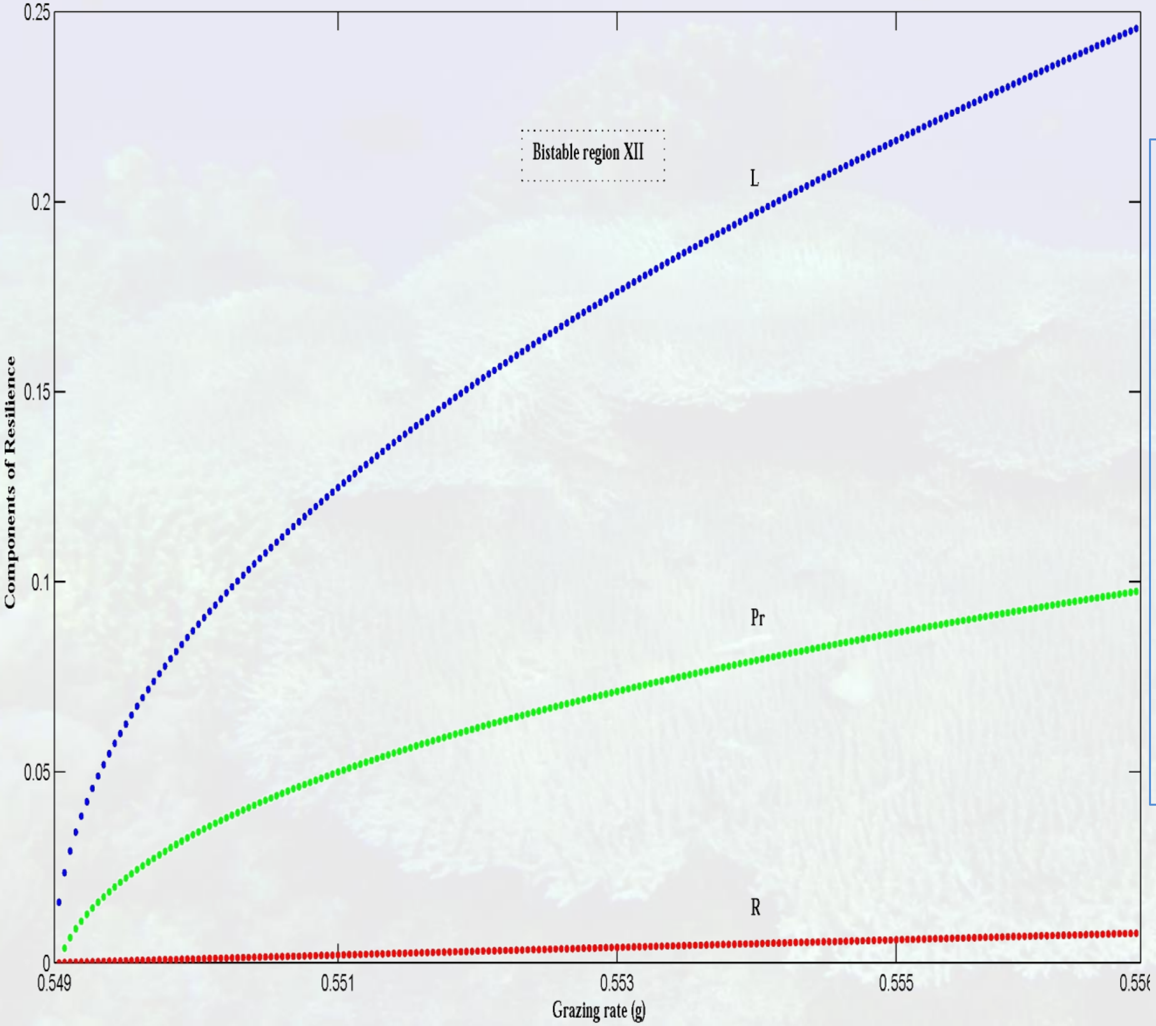
The resilience of the system at the interior equilibrium is minimum when the harvesting rate of *Parrotfish* exceeds $h = 0.0191$ and increases in the bistable region **XV** due to the decrease of harvesting rate. The resilience becomes maximum when rate of harvesting is lowered below $h = 0.0138$.

Bifurcation diagram of g vs. the equilibrium value of coral cover



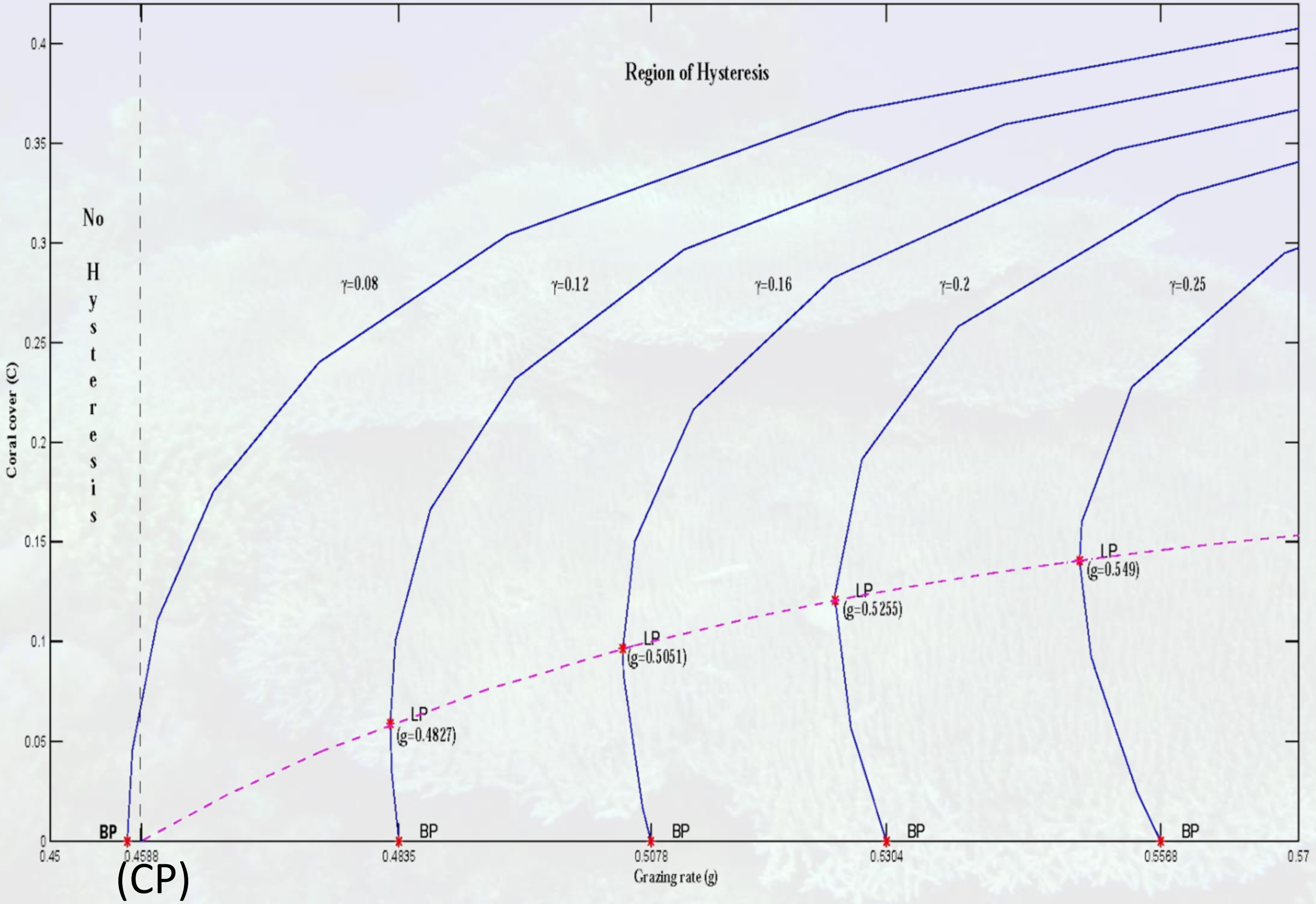
Hysteresis will result in with low grazing rate followed by an increase in the grazing rate above a critical threshold g^*

Change of Resilience at E^* due to the increase of g



The resilience of the system at the interior equilibrium is maximum when grazing intensity exceeds $g = 0.5568$ and decreases in the bistable region **XII** due to the decrease of grazing intensity. The resilience becomes minimum when grazing intensity is decreased below $g = 0.549$.

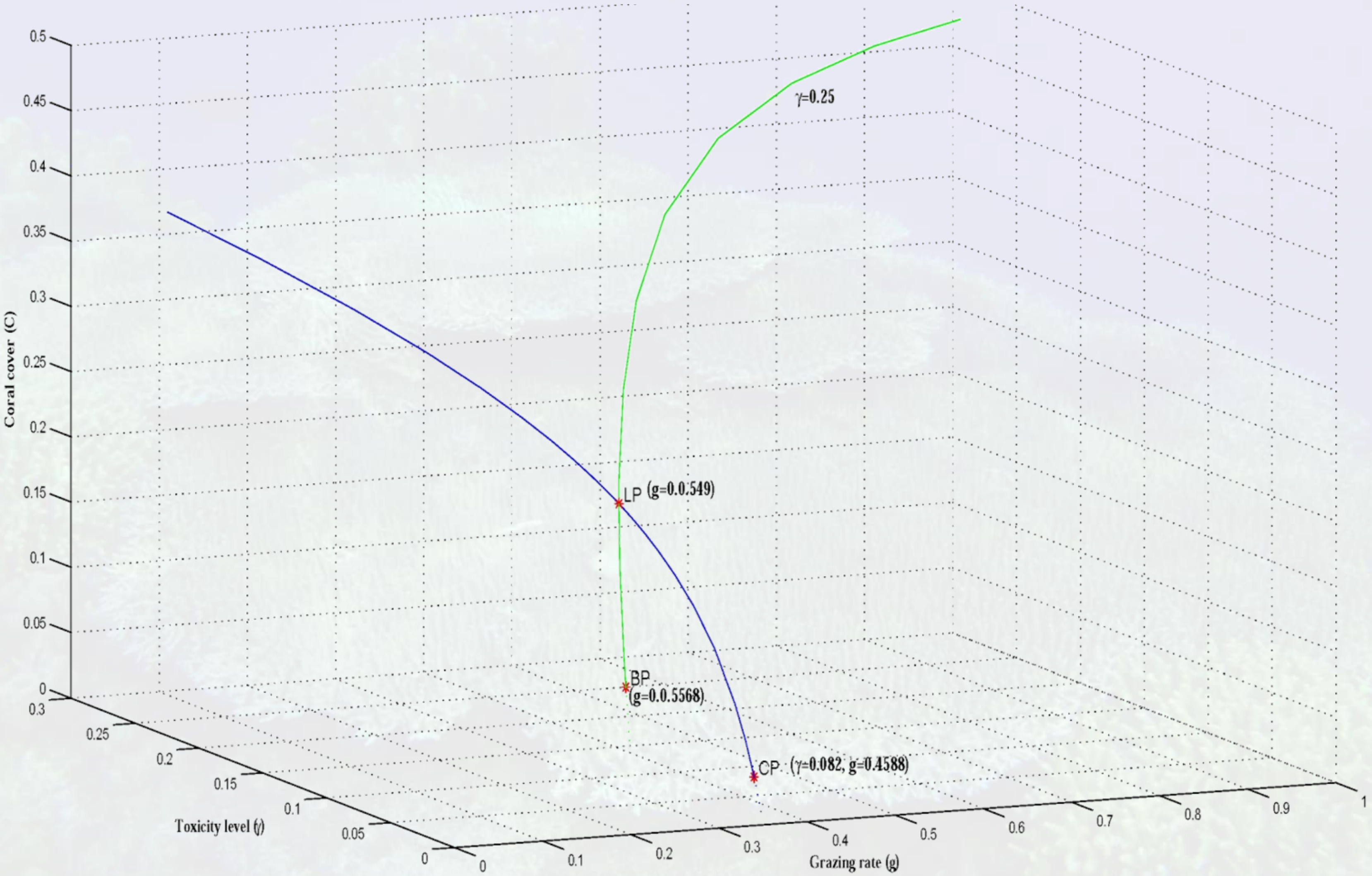
Change of Resilience at E^* due to change in g and γ



With g and γ as active parameters, the resilience of the system becomes maximum when the macroalgal toxicity is less than the threshold value $\gamma = 0.082$ where the saddle-node curve meets the parameter axis at g = 0.4588, generating a cusp point (CP) at the point of intersection.

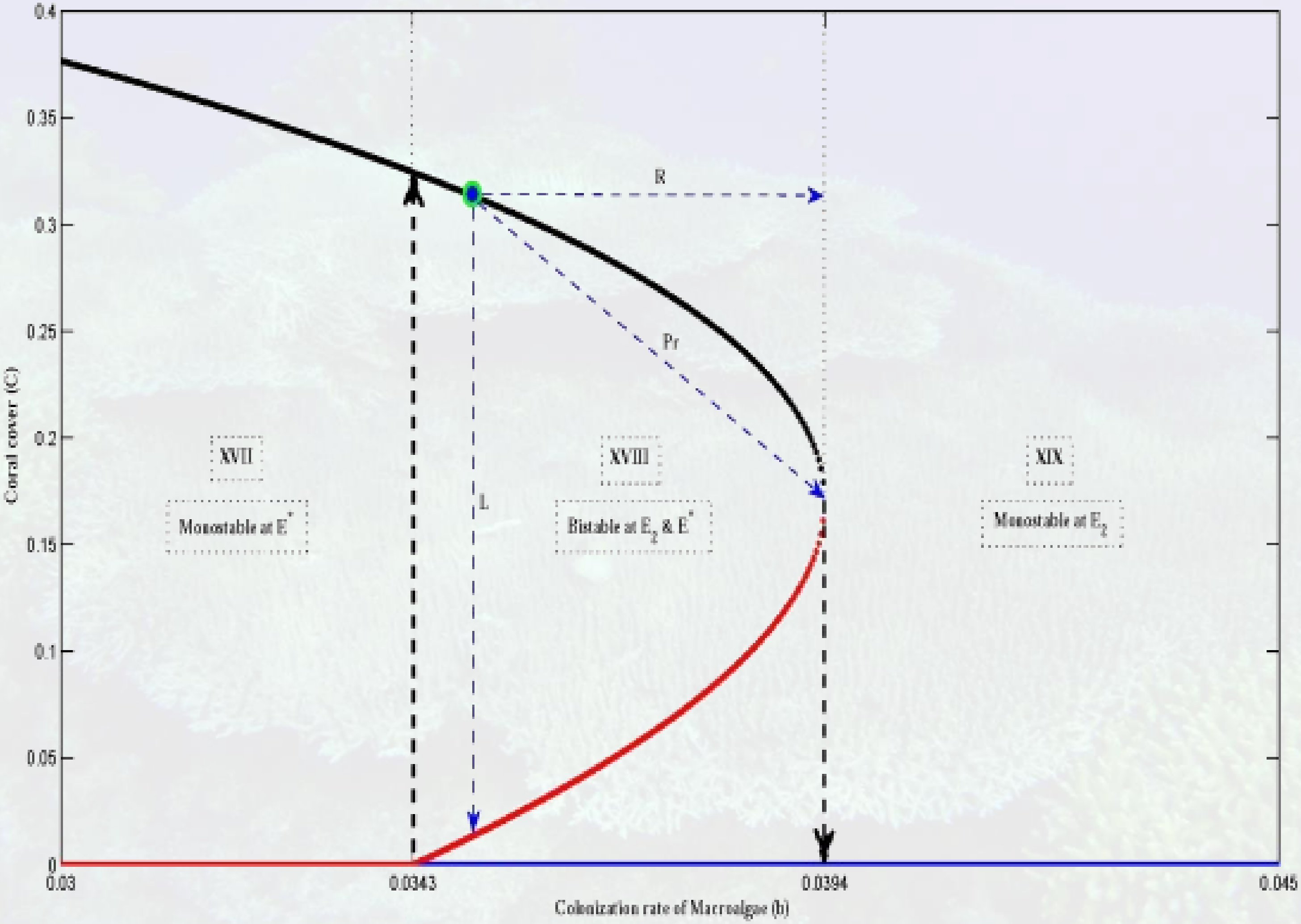
The increase of macroalgal toxicity decreases the latitude component of resilience of coral-dominated regime due to the decrease of coral cover. Also, the resistance component of resilience of coral-dominated regime is decreased even with high grazing rate of Parrotfish, measured by taking the difference of the values of g at the saddle-node bifurcating point (LP) and at transcritical bifurcating point (BP) for a particular value of γ.

Codim2 bifurcation with g and γ as active parameters



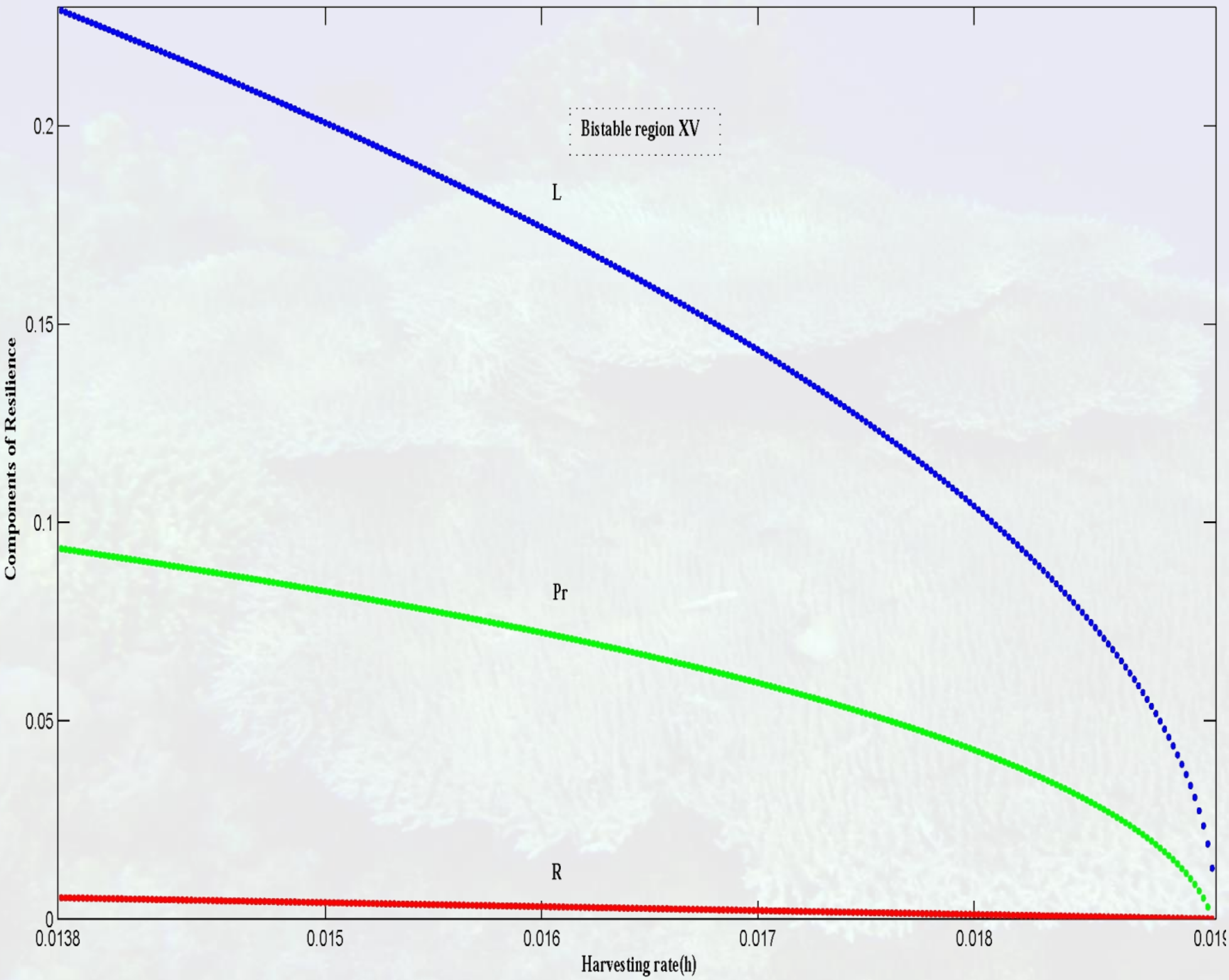
A two-parameter bifurcation diagram with g and γ as active parameters, representing a cusp point (CP) at $(g, \gamma) = (0.4588, 0.082)$ on the saddle-node curve.

Bifurcation diagram of *b* vs. the equilibrium value of coral cover



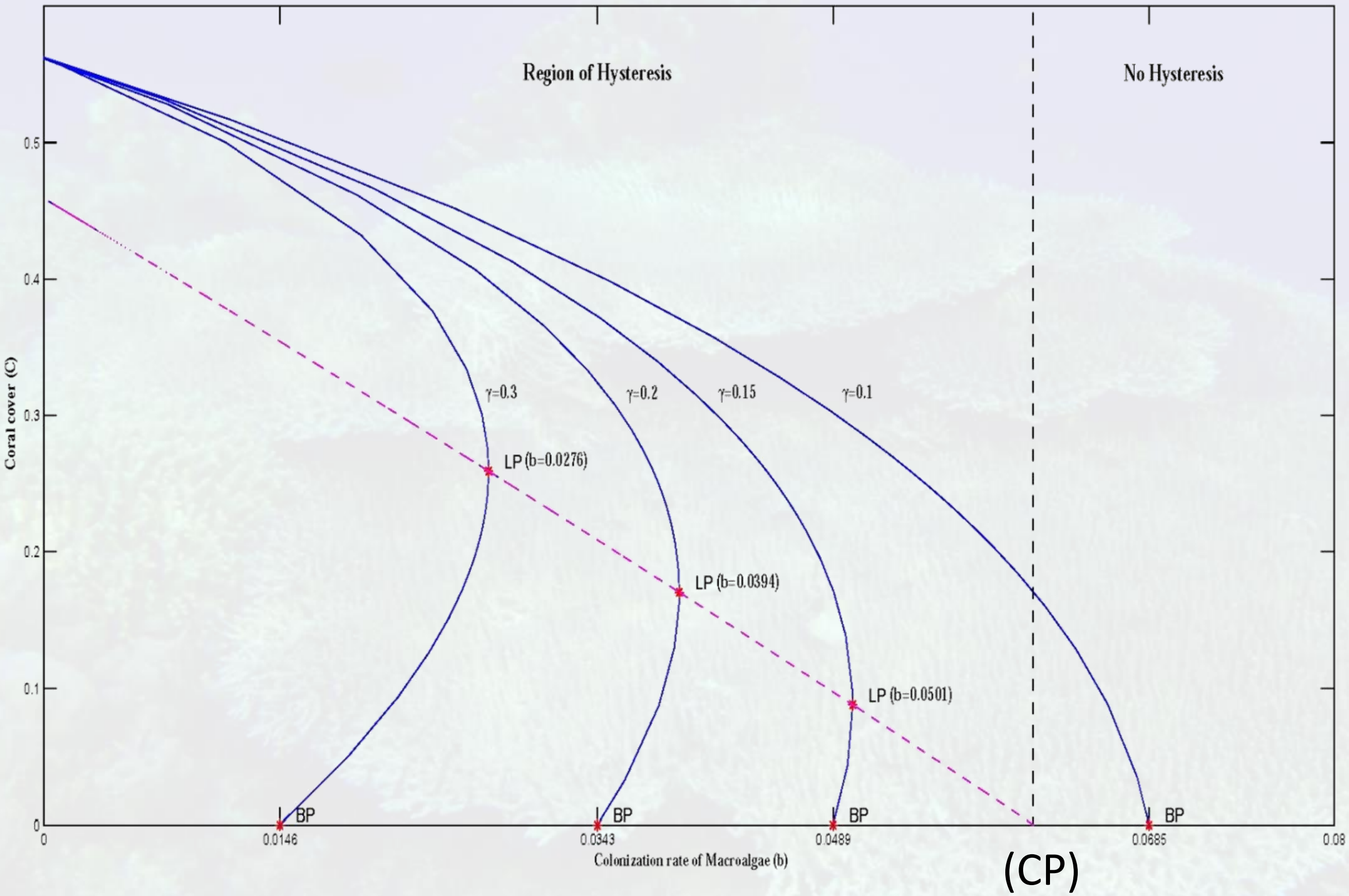
Hysteresis will result in with low colonization rate followed by an increase in the colonization rate above a critical threshold b^*

Change of Resilience at E* due to the increase of b



The resilience of the system at the interior equilibrium is minimum when the macroalgal immigration rate exceeds $b = 0.0394$ and increases in the bistable region **XVIII** due to the decrease of immigration rate. The resilience becomes maximum when rate of immigration is lowered below $b = 0.0343$.

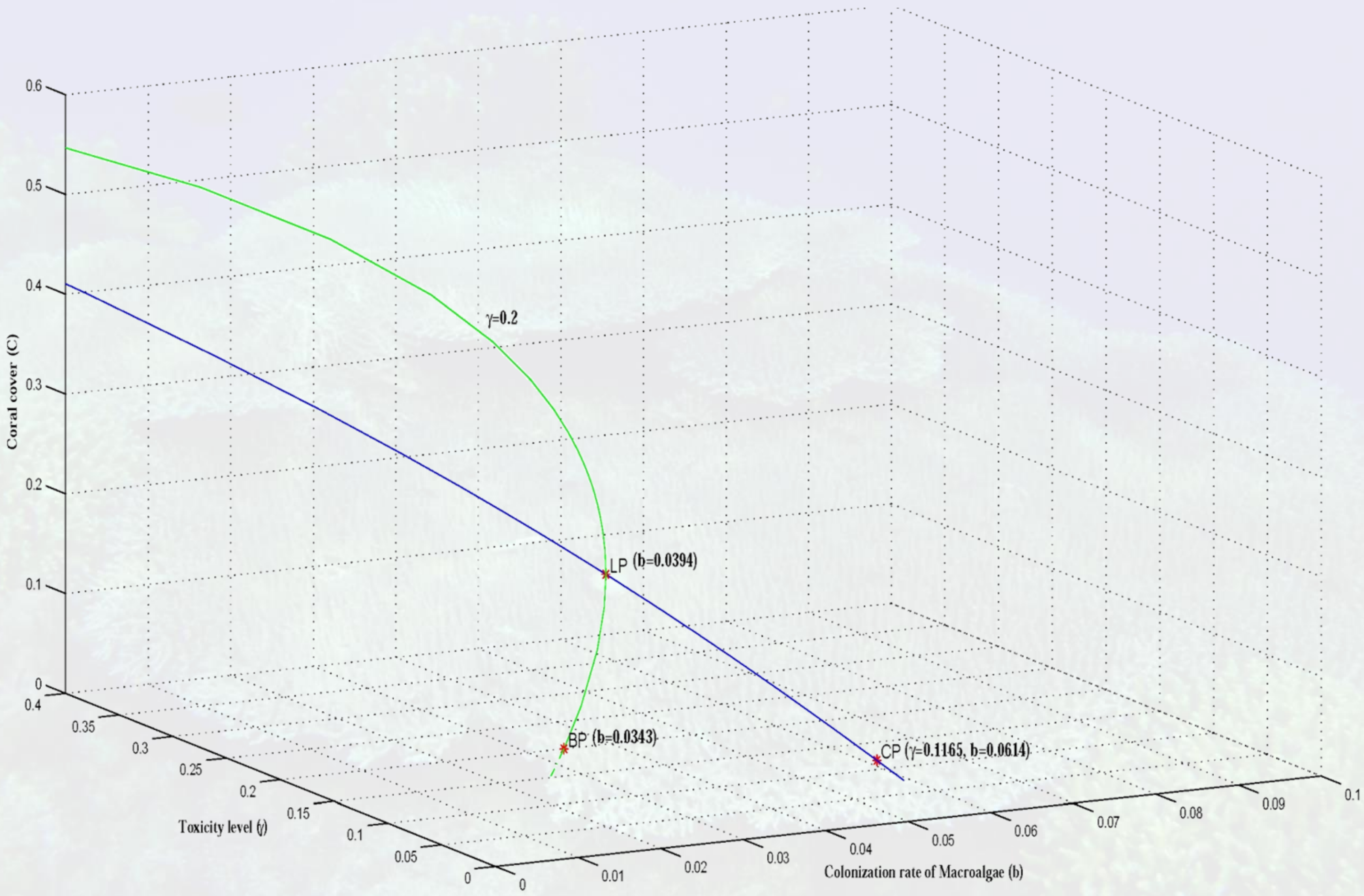
Change of Resilience at E^* due to change in b and γ



With b and γ as active parameters, the resilience of the system becomes maximum when the macroalgal toxicity level is less than $\gamma = 0.1165$ where the saddle-node curve meets the parameter axis at $b = 0.0613$, generating a cusp point (CP) at their point of intersection.

The decrease of macroalgal toxicity increases the resilience of coral-dominated regime even with the increase in colonization rate of macroalgae, measured by taking the difference of the values of b at the saddle-node bifurcating point (LP) and at transcritical bifurcating point (BP) for a particular value of γ.

Codim2 bifurcation with b and γ as active parameters



A two-parameter bifurcation diagram with b and γ as active parameters, representing the cusp point at $(b, \gamma) = (0.0613, 0.1165)$ on the saddle-node curve.

Observations

➢ Resilience of the coexistence state decreases due to

- the increase of macroalgal toxicity.
- the increase of the rate of harvesting of herbivores.
- the increase of macroalgal external immigration rate.
- the decrease of grazing intensity of herbivores.

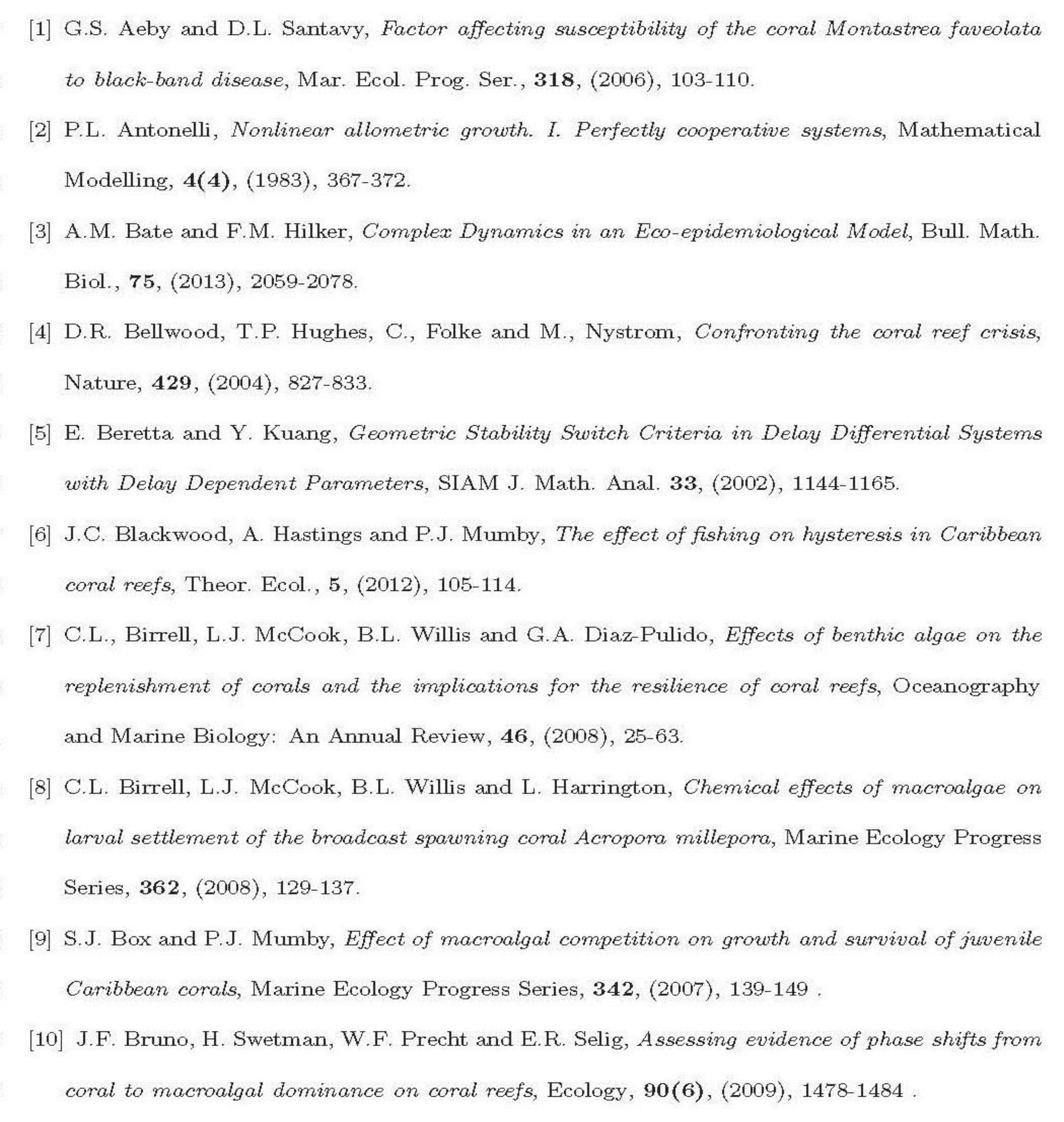
Observations (contd.)

- There is a gradual decrease in the toxicity-tolerance level of the stable coexistence state with a steady increase in harvesting rate of herbivores.

- A sharp decrease in the toxicity-tolerance level of the stable coexistence state occurs even with

- slight decrease of herbivore-grazing intensity.
- slight increase of immigration rate of toxic-macroalgae.

Reference



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THANK YOU!